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CALC-SILICATE ROCKS AT TOOLANGI, VICTORIA

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ABSTRACT: Calc-silicate rocks outcrop over a small area on Blue Mount, near Toolangi, Victoria. They were originally a sequence of calcareous mudstones and argillaceous limestones of Late Silurian-Early Devonian age, which were contact metamorphosed by a series of small granodiorite intrusions in the Late Devonian. The rocks are mainly fine-grained, pale grey hornfels with localized development of grossular-rich spheroids, aggregates and spots. Some specimens show different alteration textures, where originally dark hornfels have been altered by reaction with metamorphic fluids.

Minerals present include grossular, diopside, wollastonite, prehnite, vesuvianite, calcite, quartz, sphene, scolecite, K feldspar and plagioclase, nearly always as fine-grained aggregates. Only wollastonite and grossular develop as crystals which are visible to the naked eye.

The bulk chemistry of the rocks is variable and original compositions have been modified during metamorphism. Analyses of coexisting dark (metamorphic) and pale (metasomatized) hornfels suggest that Ca, Si, Al, S, Cl and Na were the main mobile elements, with the alteration resulting in the removal of Si, Al, Na and S from the original hornfels and the concentration of Ca, K, Fe, Mg, Ba, Sr and Cl in the resulting pale hornfels.

The calc-silicate assemblage crystallised in a metamorphic-metasomatic event in which initial prograde contact metamorphism, which may have been largely isochemical, was overlapped by metasomatism which led to the partial homogenization of the metasedimentary sequence and localized development of coarser skarn-like textures. Solutions responsible for the metasomatism were probably derived mainly from the sedimentary sequence or from meteoric sources. The lack of iron-enrichment suggests that the influence of magmatic fluids was minimal.

Comparison of the various assemblages observed in the Blue Mount rocks with those in calculated and experimentally determined equilibria suggests that the maximum temperature of the prograde metamorphism was between 500° and 550°, at pressures, estimated stratigraphically, of the order of 0.5 Kb or less. The solutions at, and following, the metamorphic peak were water-rich ($X_{\text{H}_2\text{O}} < 0.2$). Retrogression was marked by localized crystallisation of vesuvianite, prehnite and scolecite.

Calc-silicate rocks from contact metamorphic aureoles are rare in Central Victoria, reflecting the scarcity of calcareous sediments in sequences intruded by Palaeozoic granitic rocks. Small scale occurrences have been reported from the aureoles of the Bulla Granite (Tattam 1925) and the Strathbogie Batholith near Bonnie Doon (Phillips & Wall 1980). Hornfels containing calc-silicate assemblages were recorded in the Maldon goldfield (Moon 1897), while Lindner (1953) described vesuvianite and brucite from the contact of a gabbroic intrusion into the Ordovician Digger Island Limestone at Waratah Bay (recent evidence suggests this latter contact is an unconformity—Singleton pers. comm. 1984, Birch unpub. data).

Probably the most extensive suite of calc-silicate rocks occurs on Blue Mount, about 3 km south of Toolangi (Fig. 1). Kenley (1958) briefly described the geology of the area in preparation for the construction of the seismic observatory on the Mount and subsequently drafted a map of the observatory excavation. However, no additional petrological or mineralogical studies of the unusual rock-types exposed were carried out until specimens were collected for the National Museum of Victoria in 1978/9.

GEOLOGY

Interbedded Late Silurian to Early Devonian siltstones and sandstones of the Dargile and Humevale Formations (VandenBerg 1971) form the bedrock of the

area (Fig. 1). The sediments are folded with a roughly north-south axial trend. Three kilometres to the east of Blue Mount (elevation 604 m) the north-south trending Yellingbo Fault Zone brings the acid-intermediate volcanic rocks of the Acheron Cauldron Complex into contact with the basement (Dudley *et al.* 1971). Intrusion of granitic rocks associated with the complex (the Black Range composite intrusion) has resulted in a belt of contact metamorphism from 1 to 4 km wide in the basement sediments. Between Toolangi and Hcalesville, four small outcrops of granodiorite occur in a line approximating regional trends (Fig. 1). These probably represent apophyses of a larger near-surface intrusion responsible for the contact metamorphic effects.

On Blue Mount, the contact metamorphic rocks consist mainly of light grey calc-silicate hornfels. Several decomposed feldspathic dykes were mapped in the original excavation for the observatory (Kenley 1958). The full extent of the calc-silicate rocks was not determined but the outcrop appears to be restricted to Blue Mount, and probably would not exceed 1 km² in outcrop area.

PETROGRAPHY

The light grey hornfels is cherty, sometimes porcellainous, in appearance. Internal casts of shelly fossils are occasionally found. Much of the pale hornfels contains thin bands or irregular patches of a dark grey, similarly fine-grained rock. Many of the macroscopic

replacement-type textures (Figs 2, 3) suggest that the pale-coloured hornfels has resulted from alteration of the dark rock type. What appears to be original bedding is preserved locally (Fig. 4) in the form of alternating dark and light bands. In general, the pale and dark grey hornfels are too fine-grained to enable individual minerals to be distinguished in thin section. However, X-ray diffraction and electron microprobe investigations reveal that K feldspar, diopside and quartz are the dominant minerals in both rock types, with minor calcic plagioclase, grossular, wollastonite, calcite, sphene, apatite and opaques. There is little textural or mineralogical distinction between dark and light coloured rock types in thin section. However, the dark hornfels has more finely disseminated opaque grains, mainly sulphides, while the pale hornfels is more turbid in appearance.

The most noticeable features of the more massive, pale coloured hornfels are dark grey spots and clots, which are locally abundant. These range from simple circular or oval shapes up to 2 cm across, occurring either singly or as beaded groups (Fig. 5) to larger coarse-grained patches 10 to 12 cm wide. The margins of these blebs and patches are always curved and generally distinct, but in some varieties, more diffuse margins give the rock an overall mottled appearance. Often the clots resemble spherules, with distinct rim and core sections in hand specimen. On weathered surfaces, the clots stand out as small nodules. The main mineral

forming the clots is grossular, with minor wollastonite, diopside and sphene. In clots with a distinct rim and core, the rims are richer in grossular (95%) than the core (80%).

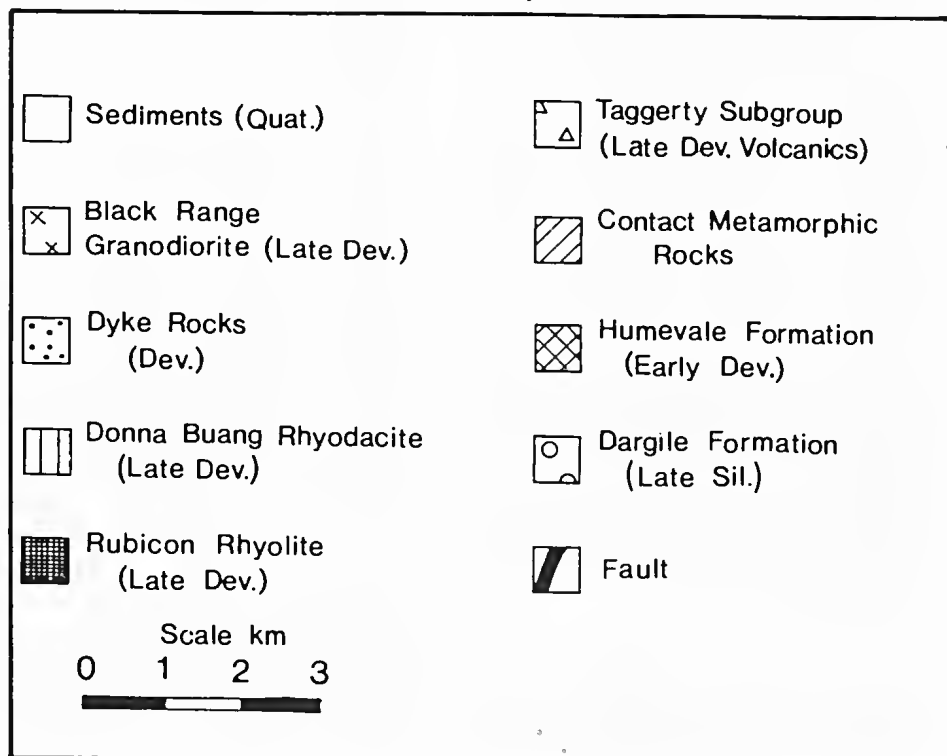
Finely laminated rock types are occasionally developed. In these and in the mottled rock types, coarser patches, of the order of several mm across, and short veinlets, are often developed. These generally contain assemblages involving wollastonite, grossular, diopside, prehnite, calcite and quartz.

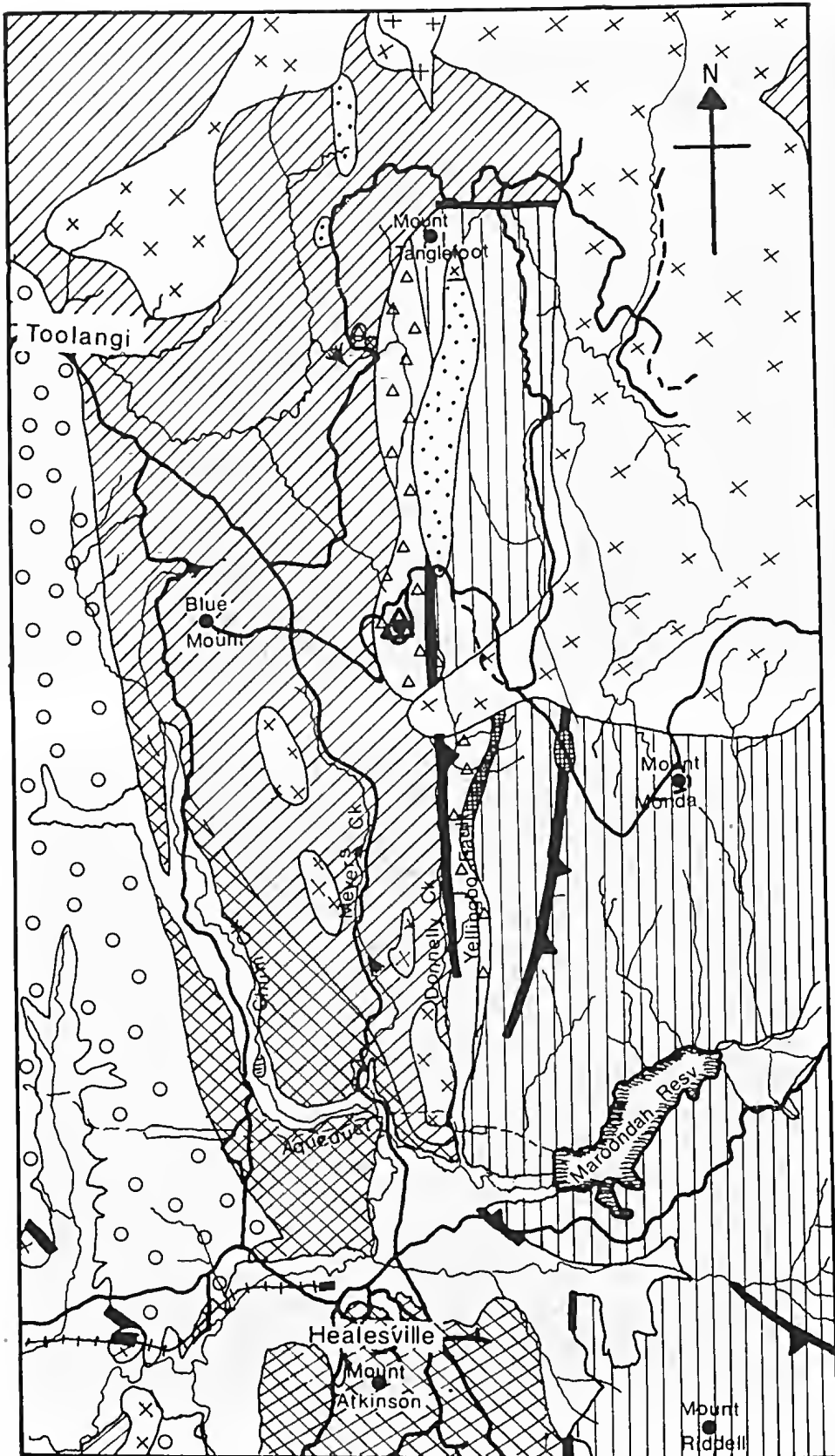
MINERALOGY

The mineralogy of the calc-silicate rocks is relatively restricted, reflecting the small size of the outcrop, the uniformity of formation conditions and, to an extent, the similarity of the original sedimentary components.

GROSSULAR: As the major constituent of the spherulitic-like clots, the grossular appears mid to dark grey, occasionally with brownish or pinkish overtones, translucent to opaque and with a greasy lustre. Where individual grains can be distinguished in thin section, the grossular is not isotropic, but shows low birefringence. In some of the coarser patches and in the mottled rock types, individual dodecahedral outlines can be distinguished, and the grossular exhibits strong twinning effects, similar to the sixling twinning observed in some occurrences of cordierite (Fig. 6). This strong similarity was probably responsible for the original description of the Blue

Fig. 1—General geological and locality map of the Healesville-Toolangi area. The calc-silicate hornfels occurs on and in the vicinity of Blue Mount.





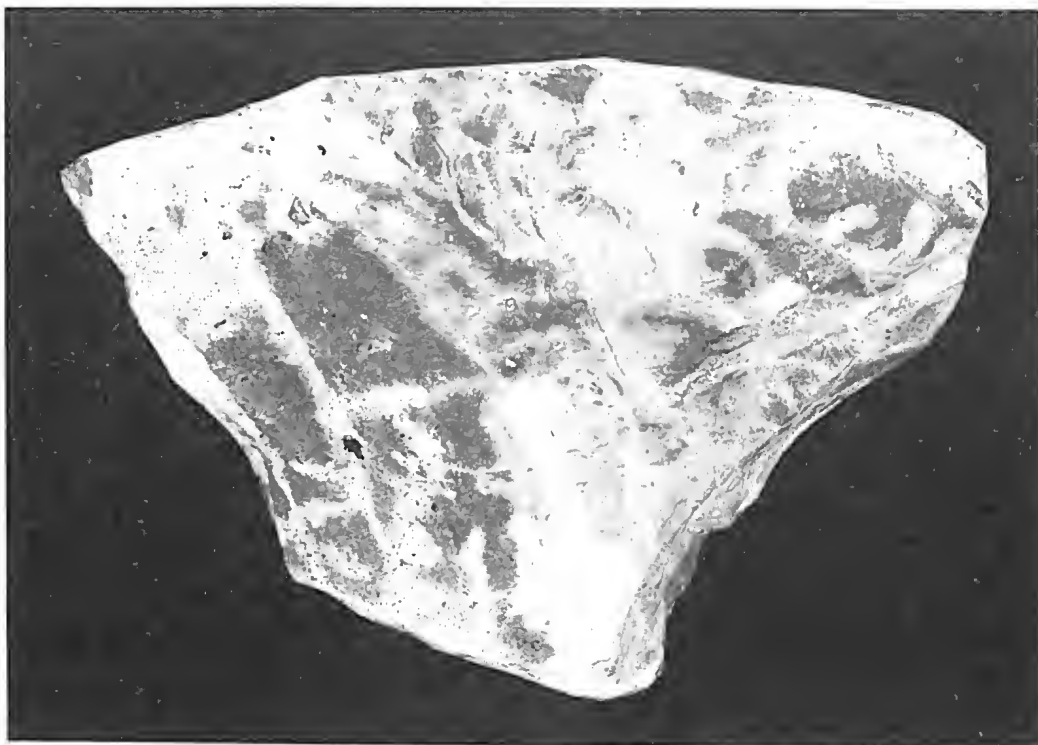


Fig. 2—Replacement texture in calc-silicate hornfels. Alteration of originally dark hornfels has proceeded via a network of fractures (NMV specimen E10549A, 8.0 cm long).

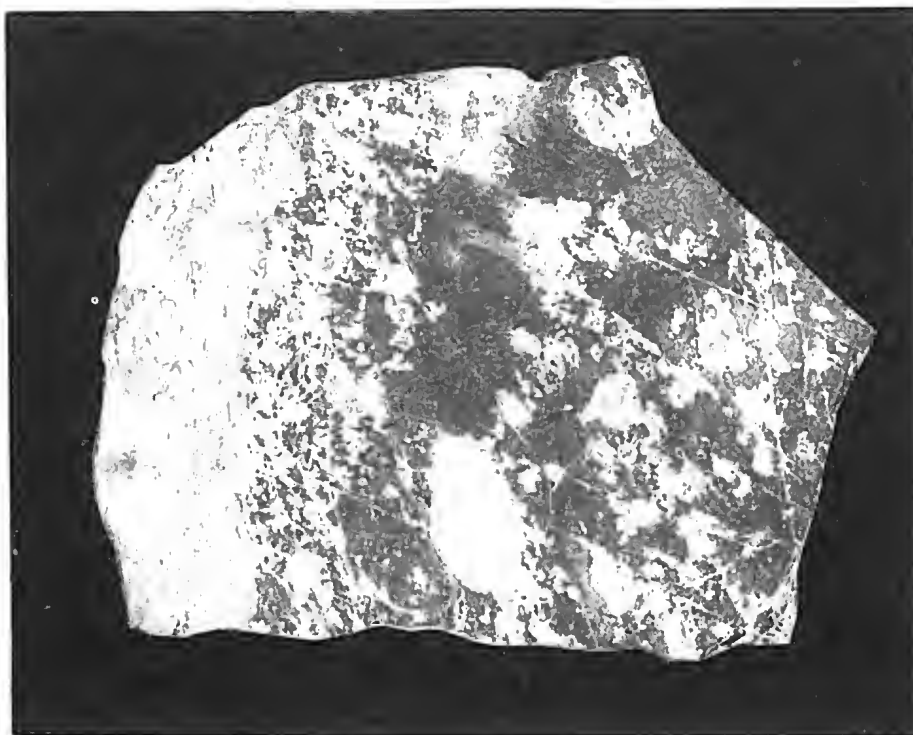


Fig. 3—Pervasive alteration texture in calc-silicate hornfels (NMV specimen E10549C, 5.5 cm long).



Fig. 4—Specimen showing remnant layers (original bedding, subsequently faulted) of unaltered dark hornfels in pale alteration product. Specimen is 8.5 cm across.



Fig. 5—Grossular blebs in pale hornfels. The largest clot is 0.5 cm across (NMV specimen E10280).



Fig. 6—Photomicrograph showing large non-isotropic grossular crystal (1 mm across) in fine-grained calc-silicate hornfels (calcite, diopside, quartz) (NMV specimen E10283).

Mount hornfels as showing local development of cordierite blebs (Kenley 1958). Anisotropism and twinning in garnets of the grossularite group is well documented (Deer *et al.* 1962). Light grey translucent grossular crystals up to 5 mm across are occasionally found lining cavities on weathered outcrop surfaces. Microprobe analysis shows the grossular to be quite uniform in composition. Pyrope and spessartite components are minimal and andradite is the main substitutional end member (Table 1). However, overall iron contents are low ($\text{Gr:Ad} > 85:15$) and are characteristic of garnet compositions in contact metamorphic rocks rather than skarns produced by magmatically-derived fluids (Einardi & Burt 1982).

WOLLASTONITE: Wollastonite is disseminated through much of the pale hornfels and is a minor constituent of the grossular spherules. When visible under the microscope, in some of the coarse-textured rocks, and in patches and veinlets in fine-grained rocks, it forms fibrous aggregates usually associated with grossular and diopside (Fig. 7). Patches of white, coarsely-crystalline fibrous wollastonite, up to 6 cm across, with individual crystals up to 2 cm long, may occur in the pale grey hornfels (Fig. 8). Microprobe analyses reveal only small amounts of Fe and Mn (Table 1).

DIOPSIDE: Diopside is present in all rock types, as clouds of tiny, euhedral, equidimensional crystals included in most of the other minerals. Larger diopside crystals occur in patches of grossular and wollastonite in the coarser-textured rocks. Thin veinlets consisting of diopside and quartz occur surrounded by narrow bleached zones in some of the hornfels (Fig. 9). Microprobe

TABLE 1
ELECTRON MICROPROBE ANALYSES OF GROSSULAR AND WOLLASTONITE IN THE BLUE MOUNT CALC-SILICATE ROCKS.

Wt%	1	2	3
SiO ₂	38.64	38.85	52.21
TiO ₂	0.80	0.36	0.12
Al ₂ O ₃	20.99	18.48	0.08
Fe ₂ O ₃	2.30	6.88	—
FeO	—	—	0.43
MnO	0.14	0.04	0.09
MgO	0.03	0.02	—
CaO	37.50	36.59	47.68
Na ₂ O	—	0.05	—
K ₂ O	—	—	—
BaO	0.08	0.14	—
Total	100.48	101.41	100.61
Structural Formulae			
(16 cats, 24 'O') (4 cats, 6 'O')			
Si	5.848	5.899	2.004
Ti	0.091	0.041	0.003
Al	3.745	3.308	0.004
Fe ³⁺	0.262	0.786	—
Fe ²⁺	—	—	0.014
Mn	0.018	0.005	0.003
Mg	0.007	0.005	—
Ca	6.082	5.953	1.961
Na	—	—	—
K	—	—	—
Ba	0.005	0.008	—

1, Grossular (E10283); 2, Grossular (E10280); 3, Wollastonite (E10280).

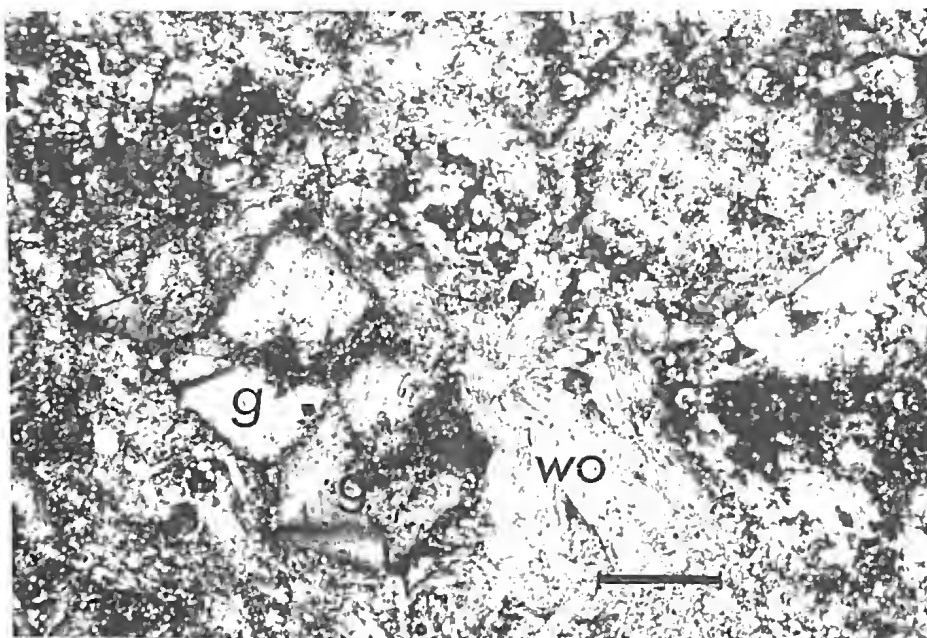


Fig. 7—Fibrous wollastonite (wo) associated with grossular (g) and small diopside crystals (NMV specimen E10282). Scale bar = 0.5 mm.

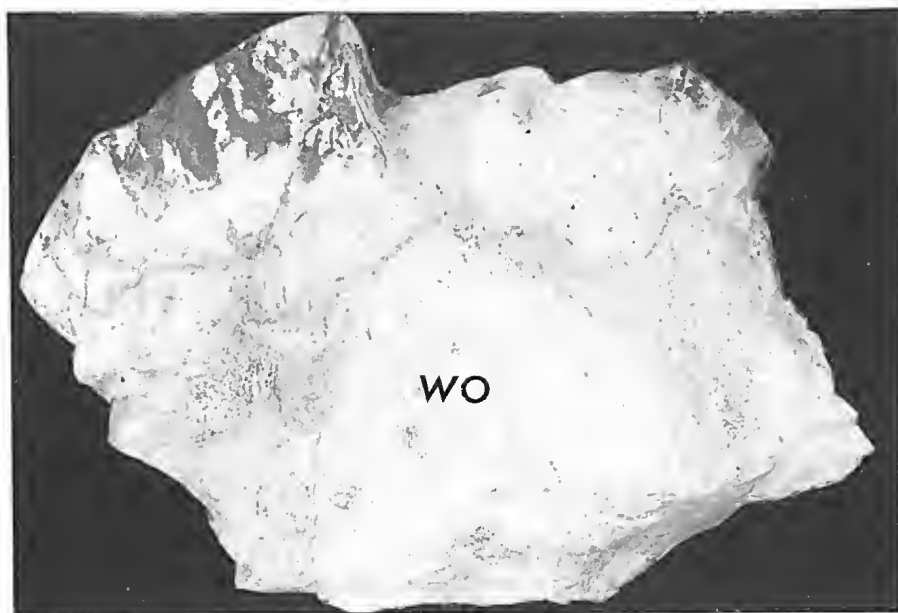


Fig. 8—Patch of coarse wollastonite 4.5 cm across in fine-grained calc-silicate hornfels (NMV specimen M34812).

TABLE 2
ELECTRON MICROPROBE ANALYSES OF DIOPSIDE AND SPHENE IN
THE BLUE MOUNT CALC-SILICATE ROCKS.

Wt%	1	2	3
SiO ₂	51.96	51.89	30.99
TiO ₂	0.08	0.10	36.90
Al ₂ O ₃	0.13	0.44	3.09
Fe ₂ O ₃	0.87	—	—
FeO	11.51	15.34	0.13
MnO	0.73	0.20	—
MgO	9.86	8.00	0.05
CaO	24.86	24.24	28.35
Na ₂ O	0.10	0.11	—
Cr ₂ O ₃	0.07	0.11	—
H ₂ O calc.	—	—	1.18
Total	100.17	100.43	100.69
Structural Formulac			
	(4 cations, 6 oxygens)	(12 cats, 20 'O', 1[OH,F])	
Si _{iv}	1.985	1.998	3.937
Al _{vi}	0.006	0.002	0.063
Al	—	0.018	0.400
Ti	0.002	0.003	3.525
Fe ³⁺	0.025	—	—
Fe ²⁺	0.368	0.494	0.014
Mn	0.024	0.007	—
Mg	0.562	0.459	0.009
Ca	1.018	1.000	3.859
Na	0.007	0.008	—
Cr	0.002	0.003	—
OH	—	—	1.000

1, Diopside in quartz-diopside veinlet (E10547); 2, Diopside crystal (E10282); 3, Sphene crystal (E10281).

analysis reveals a relatively narrow compositional range, with Mg/(Fe+Mg) varying between 0.66 and 0.48 (Table 2).

K FELDSPAR: K feldspar is the main mineral in many of the pale grey porcellainous rock types. However, due to its variable abundance and extremely small grain size (<0.05 mm) precluding optical detection, X-ray powder diffraction is the simplest method of determining both its relative abundance and composition. The latter can only be determined where quartz is virtually absent, as the 201 reflection for K feldspar is overlapped by the proportionally much stronger 101 reflection for quartz. K feldspar compositions in specimens of the pale-grey hornfels were estimated to range from Or₈₅Ab₁₅-Or₉₂Ab₈, using the 201 method of Wright (1968). Microprobe analysis was limited by the small grain size, but analyses confirmed the composition estimated from the X-ray diffraction data. Small amounts of both Ba and Ca were detected (Table 3). Attempts to determine K feldspar compositions by X-ray diffraction in coexisting pale and dark regions were hampered by an abundance of quartz in either one or both portions. Microprobe analyses however indicate that alkali feldspars in the dark fraction are variable in composition, and are less potassic and more calcic than those in the pale regions (Table 3).

The structural states of feldspars were determined using the three-peak method of Wright (1968). The 060 and 204 reflections for K feldspar are not obscured by quartz peaks and their positions were measured whenever K feldspar was sufficiently abundant. Using a quantifying method developed by Ragland (1970), K feldspars in the pale rock types were shown to have structural states very close to that of orthoclase, but



Fig. 9—Thin diopside-quartz veinlet surrounded by an alteration zone 2.5 mm wide, in dark hornfels (NMV specimen E10547).

TABLE 3
ELECTRON MICROPROBE ANALYSES OF FELDSPARS IN THE BLUE MOUNT CALC-SILICATE ROCKS

Wt%	1	2	3	4	5
SiO ₂	65.32	64.36	64.96	64.59	57.00
Al ₂ O ₃	18.93	19.14	19.94	19.60	24.31
Fe ₂ O ₃	0.08	0.29	0.24	0.19	0.46
MgO	—	—	0.05	0.07	—
CaO	—	0.06	1.76	3.23	10.76
Na ₂ O	0.94	0.62	6.27	3.19	2.95
K ₂ O	14.64	14.87	5.65	8.80	2.38
BaO	0.96	0.70	0.26	0.24	0.25
Total	100.87	100.04	99.13	99.91	98.11
Endmember Compositions (mol.%)					
Or	89.5	92.5	33.8	53.6	14.9
Ab	8.7	5.9	56.9	29.5	28.1
An	—	0.3	8.8	16.5	56.5
Cel	1.8	1.3	0.5	0.4	0.5

1, K feldspar in pale, finegrained rock (E10280); 2, K feldspar in pale fraction (E10544); 3, Alkali feldspar in dark fraction (E10544); 4, Alkali feldspar in dark fraction (E10544); 5, Plagioclase in dark fraction (E10547).

with between 5-10% of ordering towards maximum microcline. K feldspars in the dark fraction were always slightly more ordered, with about 20-25% ordering towards maximum microcline. These data are shown in Table 4 and Fig. 10. It can therefore be concluded that the process which partially or completely altered the dark hornfels, has resulted in the development of a more disordered, more potassic feldspar in the pale alteration zones.

PLAGIOCLASE: X-ray diffraction revealed that plagioclase is present in most of the fine-grained rock types, but as a minor mineral only. Microprobe analyses suggest it is mainly labradorite (Table 3).

QUARTZ: The abundance of quartz varies, reaching a maximum in some of the dark hornfels. It is absent from the spherule-bearing porcellainous variety. In the fine-

grained hornfels it forms small anhedral grains, possibly representing original recrystallized detrital fragments. Patches of interstitial quartz are associated with larger grains of grossular, wollastonite, diopside, vesuvianite, prehnite and calcite in the coarser-textured rocks. Small quartz-diopside veinlets are evidence for mobilization of Si during metamorphism (Fig. 9).

CALCITE: Calcite is most prominent in the coarser-textured rocks, where it forms interstitial patches. It generally encloses small diopside inclusions and may coexist with nearly all other minerals, including quartz. It is absent or a minor phase only in many of the fine-grained hornfels.

VESUVIANITE: Vesuvianite occurs in several rock types, forming either blocky crystals resembling phenocrysts or pale brown zoned prismatic crystals (Fig. 11). In both cases, the maximum crystal length is about 1.5 mm. Microprobe analyses (Table 5) on the blocky crystals and the cores of the pale brown prisms are similar. Fe/Mg ratios are variable and the vesuvianite contains about 1.4% TiO₂ and between 1 and 2% F. The rims of the prismatic crystals have an unusual composition (Table 5) with more structural water, and do not recalculate to a vesuvianite structural formula. The identity of this phase is unknown.

PREHNITE: Prehnite is widespread in coarser-grained rock types as irregular grains showing bright interference colours. It appears to be an interstitial, late-crystallizing mineral. A typical microprobe analysis is shown in Table 6.

SPHENE: Small crystals of sphene occur in the rims of the grossular blebs, in the matrix of the fine-grained hornfels and in the coarser-textured rock types. The very small crystal size (about 0.03 mm) makes the determina-

TABLE 4
K FELDSPAR STRUCTURAL STATE EXPRESSED AS PERCENTAGE ORDERING TOWARDS MAXIMUM MICROCLINE FROM ORTHOCLASE

Sample	Dark	Light	Comp. (est.)
E10713	—	9	—
E10280	—	6	Or ₈₈ Ab ₁₂
E10547	21	—	—
E10549C	24	6	Or ₉₄ Ab ₆ (light)
E10549B	20	7	Or ₉₅ Ab ₅ (light)
E10544	20	11	Or ₉₅ Ab ₅ (light)
E10549A	42	27	—

NOTES ON METHOD: Two smear mounts of each sample were run in duplicate using Ni-filtered CuK_α radiation, with a chart speed of 2 cm/minute and a scanning rate of 0.25°/minute. KBrO₃ was used as an internal standard for the three peak positions measured.

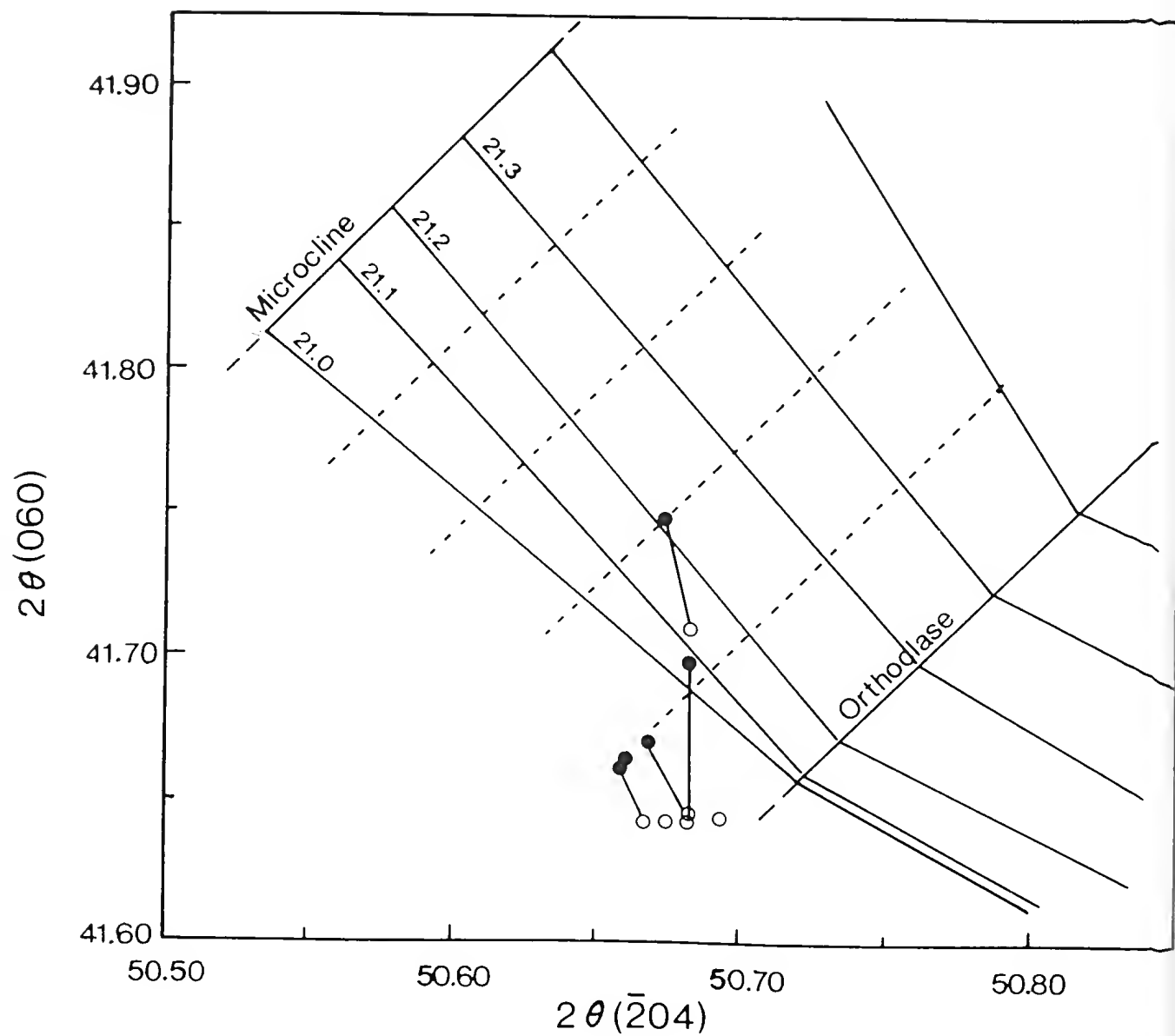


Fig. 10— $2\theta_{\bar{2}04}$ — $2\theta_{060}$ plot for K feldspars in specimens of the fine-grained calc-silicate rocks (see also Table 4 and text for discussion). Feldspars coexisting in dark (full circles) and pale hornfels (open circles) are joined by tie-lines.

TABLE 5
ELECTRON MICROPROBE ANALYSES OF VESUVIANITE IN THE BLUE
MOUNT CALC-SILICATE ROCKS

Wt%	1	2	3
SiO ₂	35.90	35.58	38.57
TiO ₂	1.55	1.40	1.81
Al ₂ O ₃	15.19	16.23	14.09
FeO	3.51	4.14	2.94
MnO	—	0.06	0.10
MgO	2.61	1.33	0.72
CaO	35.80	36.07	25.38
Na ₂ O	0.04	0.09	0.05
BaO	—	—	0.79
F	0.82	1.08	0.16
Cl	—	0.61	0.16
*H ₂ O	2.05	1.77	0.10
-O = F, Cl	0.34	0.59	0.10
Total	97.13	97.77	84.87
Structural Formulae (25 cations, 38 oxygens, 4 OH)			
Si	8.840	8.763	—
Al	4.409	4.710	—
Ti	0.287	0.259	—
Fe ²⁺	0.722	0.853	—
Mn	—	0.012	—
Mg	0.958	0.487	—
Ca	9.444	9.517	—
Na	0.018	0.045	—
Ba	—	—	—
F	0.637	0.841	—
Cl	—	0.254	—
OH	3.363	2.905	—

1, Vesuvianite crystal (E10545); 2, Core of pale brown crystal (E10282); 3, Unknown phase rimming 2.

* Calculated

tion of physical properties difficult. A microprobe analysis is shown in Table 2.

SCOLECITE: This calcium-rich zeolite is rare, with only two small crystals detected by microprobe (Table 6).

OTHER MINERALS: Very rare grains of yttrium phosphate were encountered during microprobe work. They are probably xenotime and may be detrital in origin. Several minute grains of chromite may have a similar origin. Pyrrhotite and arsenopyrite are the most abundant of the opaque minerals present, occasionally forming patches up to 2 mm across, but usually microscopical. Galena and sphalerite have been observed as small blebs up to 2 mm across and galena occasionally forms ragged grains in the core of spots.

MINERAL EQUILIBRIA

DARK HORNFELS WITH PALE ALTERATION: X-ray diffraction patterns were used to determine the mineralogy of five samples of fine-grained hornfels in which dark and pale fractions coexisted. The results are summarized in

Table 7. In three samples (E10544, E10549B & C) the quartz content in the initial assemblage (quartz, diopside, K feldspar, plagioclase, minor grossular) was reduced by the alteration. The only sample containing detectable calcite (E10549A) appeared largely unaffected.

There is no evidence remaining for the reactions producing K feldspar and diopside in the dark hornfels, as the reactants were consumed during prograde metamorphism. However, the most commonly observed reactions in siliceous carbonate rocks containing small amounts of Mg and Fe (defined approximately by the system CaO-MgO-SiO₂-H₂O-CO₂, e.g. Kerrick 1974) are:

1. dolomite + quartz → diopside + 2 CO₂ (Rice 1977)
2. tremolite + 3 calcite + 2 quartz → 5 diopside + 3 CO₂ + H₂O
3. muscovite + 6 quartz + 2 K⁺ → 3 K feldspar + 2 H₂O + 2 H⁺

In the dark hornfels, the formation of small amounts of grossular was probably controlled by the equilibrium:

4. 2 calcite + anorthite + quartz → grossular + 2 CO₂ (Gordon & Greenwood 1971).

TABLE 6
ELECTRON MICROPROBE ANALYSES OF PREHNITE AND SCOLECITE
IN THE BLUE MOUNT CALC-SILICATE ROCKS

Wt%	1	2
SiO ₂	44.36	59.64
TiO ₂	0.03	—
Al ₂ O ₃	23.67	17.23
FeO	0.23	0.07
CaO	26.84	8.77
Na ₂ O	0.06	0.46
K ₂ O	—	0.28
BaO	0.14	0.06
Total	95.33	86.51
Structural Formulae (22 'O') (72 'O')		
Si	6.110	26.855
Al	3.843	9.147
Ti	0.003	—
Fe	0.026	0.027
Ca	3.961	4.232
Na	0.008	0.400
K	—	0.162
Ba	0.007	0.011

1, Prehnite (NMV E10282); 2, Scolecite (NMV E10282).

The amount of grossular formed would be determined by the amount of calcite present initially, as this appears to have been the least abundant reactant in the hornfels. The most obvious change in the fine-grained hornfels, that of colour, is due primarily to the oxidation of sulphides, and possibly carbonaceous matter.

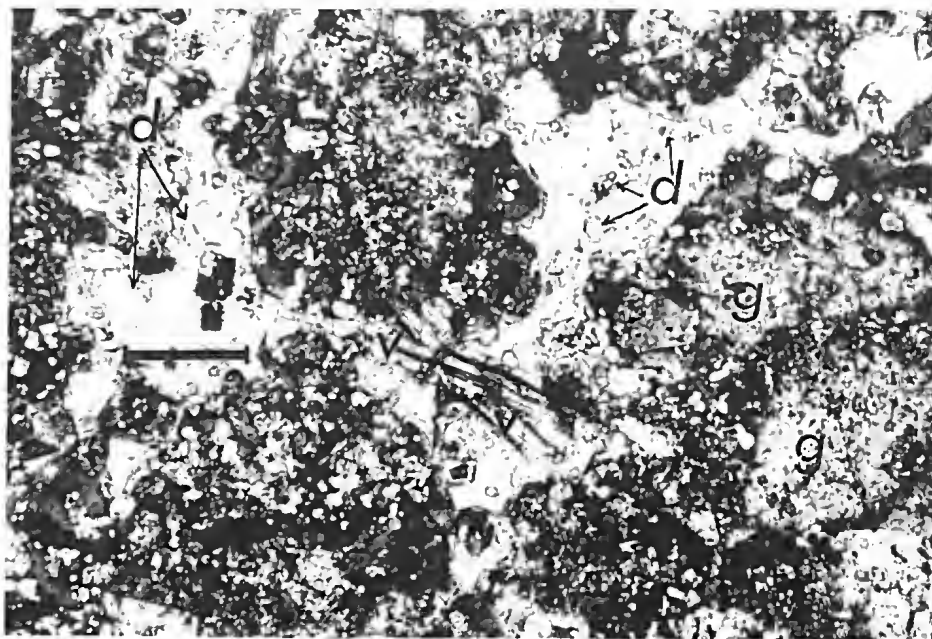


Fig. 11 — Prismatic vesuvianite crystals (v) in calcite patches associated with grossular (g) and diopside (d) (NMV specimen E10282). Scale bar = 0.5 mm.

COARSE-GRAINED ROCKS AND PATCHES: The mineralogy of coarse-textured rocks, and coarsely-crystallized patches in some of the fine-grained rocks, is relatively uniform. The following assemblages have been observed in thin section:

grossular + calcite + quartz + prehnite
 grossular + wollastonite
 diopside + sphene
 wollastonite + quartz + calcite
 vesuvianite + quartz + grossular
 vesuvianite + calcite
 calcite + prehnite + wollastonite + grossular +
 scolecite + sulphides

In some cases it is difficult to decide exactly what is an "assemblage" as textural relationships are not always clear. Thus, nearly all phases in the above assemblages contain clouds of minute diopside crystals, but these are considered to be early-formed and not necessarily part

of any equilibria close to the peak of metamorphism. K feldspar and plagioclase (ss) coexist with these assemblages in the enclosing matrix.

As well as reaction 4, there are a number of other equilibria involving the observed phases and which may have been responsible for these assemblages. In approximate order of increasing temperature, these are:

5. vesuvianite + 4 quartz → 5 grossular + 3 diopside + wollastonite + 4H₂O (Hochella *et al.* 1982)
6. prehnite → anorthite + wollastonite + H₂O (Liou 1971)
7. calcite + quartz + rutile → sphene + CO₂ (Jacobs & Kerrick 1981)
8. calcite + quartz → wollastonite + CO₂ (Greenwood 1967)
9. grossular + quartz → 2 wollastonite + anorthite (Newton 1966)
10. calcite + anorthite + wollastonite → grossular + CO₂ (Gordon & Greenwood 1971)

TABLE 7
 MINERALOGY OF FINE-GRAINED HORNFELS WITH DARK AND PALE FRACTIONS

Sample	Dark	Assemblages (main phases) Light	Main change
E10547	Q + Di + P + K	Q + Di + P + K(tr)	K reduced
E10549A	Cc + K + Di + P + Q + Gr(tr)	K + Cc + Di + P + Q + Gr(tr)	Largely unaffected
E10549B	Q + K + P + Di + Gr	K + Di + P + Q + Gr	Q reduced
E10549C	K + Di + P + Q + Gr	K + Di + P + Gr	Q removed
E10544	Q + K + Di + P + Gr(tr)	K + Di + Q + P + Gr(tr)	Q reduced

Q, Quartz; Di, Diopside; P, Plagioclase; K, K feldspar; Gr, Grossular; Cc, Calcite.

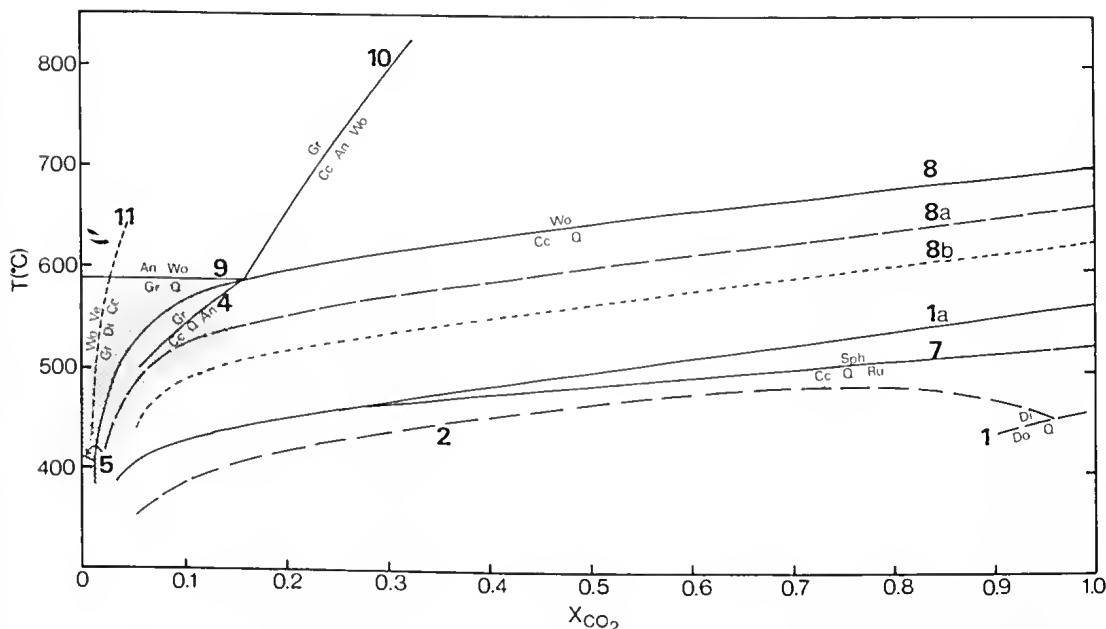


Fig. 12— T - X_{CO_2} plot of the various equilibria controlling the mineralogy of the Blue Mount calc-silicate rocks. Reactions are numbered as they appear in the text. The section as shown is not isobaric. Equilibria 1a, 4, 5, 7, 8, 9 and 10 are at 2 Kb; equilibria 1, 2 and 8a at 1Kb and equilibria 11 and 8b at 0.5 Kb. Positions of the reactions 8 and 8a are from Jacobs and Kerrick (1981) and of 8b from Williams-Jones (1981). They are plotted to illustrate the marked effect of pressure on the calcite + quartz \rightarrow wollastonite + CO_2 equilibrium. The shaded area represents the region in which the main phases crystallised.

11. 5 grossular + 4 diopside + 6 calcite + $4\text{H}_2\text{O} \rightarrow 6$ wollastonite + vesuvianite + 6 CO_2 (Williams-Jones 1981)
12. 2 grossular + 2 diopside + wollastonite + calcite + 2 $\text{H}_2\text{O} \rightarrow$ vesuvianite + 2 quartz + CO_2 (Ito & Arem 1970).

Equilibrium curves for most of these reactions are reasonably well known, either from thermodynamic calculations or experimental data. They are shown in the T - X_{CO_2} plot of Fig. 12. On this diagram, pressures for each equilibrium vary from 0.5 Kb (reaction 11), through 1 Kb (reactions 1 & 2) to 2 Kb (reactions 4, 7, 8, 9, 10). The invariant point formed by the intersection of reactions 4, 8, 9 and 10 and marked by the assemblage grossular + anorthite + wollastonite + calcite + quartz (+ CO_2) lies close to 600°C at 2 Kb. This assemblage is present on the scale of a thin section in many of the Blue Mount rocks and appears to represent conditions close to the peak of metamorphism. The marked effect of pressure on the topology of reaction 8, shown in Fig 12, suggests that the invariant point may be somewhat lower, around 550°C , for pressures as low as 0.5 Kb.

The stability relations of vesuvianite (idocrase) were investigated by Ito and Arem (1970), Shoji (1971) and Hochella *et al.* (1982). However, agreement between these studies is limited, due to the complexity of the substitutional chemistry of vesuvianite and the sensitivity of stability fields to varying starting compositions. The lower temperature stability limits of (Mg-rieht) vesuvianite is significantly reduced by the presence of quartz,

to around 380°C at $P_{\text{H}_2\text{O}} = 1$ Kb, with respect to the assemblage grossular + diopside + wollastonite (Hochella *et al.* 1982). The upper stability limit, above which melilite and monticellite are reaction products, was determined to be around 700°C (Ito & Arem 1970) or 800°C (Hochella *et al.* 1982). The absence of these minerals at Blue Mount sets an upper temperature limit of 700°C . The prehnite decomposition equilibrium (reaction 6) has been determined to lie at 440°C at 1 Kb (Liou 1971). Thus the prehnite observed is most likely to represent retrograde crystallization. This conclusion is supported by the coexistence of prehnite and scolecite in one coarse grained patch.

SPHERULE-BEARING ROCKS: The assemblage in the spheroidal blebs (essentially grossular-wollastonite-diopside-sphene) indicates that reactions 4, 7 and 8 were instrumental in their formation. The contrasting mineralogy between spherules and matrix suggests that the former were originally calcite-quartz-calcic plagioclase-rutile inclusions in a more micaceous, i.e., K-rich, host. However, the spherulitic forms appear to represent nucleation and growth rather than merely isochemical reactions within inclusions.

CHEMISTRY OF THE BULK ROCKS

Three representative Blue Mount rock types and the coexisting pale and dark fractions from sample E10544 were analysed by conventional XRF and wet chemical (for Fe^{2+}) techniques. In addition, a fine-grained sample

TABLE 8
CHEMICAL ANALYSES OF CALC-SILICATE ROCKS FROM BLUE MOUNT (1-5) AND BONNIE DOON (6)

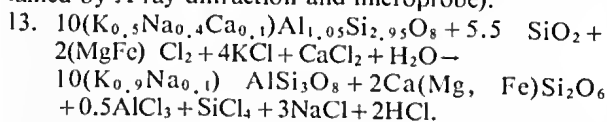
Wt%	1	2	3	4	5	6
SiO ₂	65.12	59.12	51.12	46.04	48.82	49.45
TiO ₂	0.24	0.67	0.57	0.48	0.58	0.44
Al ₂ O ₃	14.30	11.59	11.99	10.95	12.76	8.95
Fe ₂ O ₃	0.68	0.56	0.10	1.12	1.74	—
FeO	2.94	4.90	3.84	3.43	3.70	3.43
MnO	0.03	0.08	0.07	0.09	0.09	0.07
MgO	2.35	2.85	2.52	2.91	2.69	3.15
CaO	4.29	10.42	22.72	30.24	20.85	29.48
Na ₂ O	2.33	1.71	1.30	0.05	0.51	4.97
K ₂ O	4.35	5.47	2.44	0.07	4.50	0.94
P ₂ O ₅	0.15	0.17	0.09	0.10	0.10	0.08
Ig. Loss	nd	nd	nd	4.01	nd	nd
Total	97.28	97.59	96.76	99.49	96.34	100.96
ppm						
V	99	82	85	75	100	62
Cr	120	106	113	219	249	121
Ba	1696	2464	970	31	3724	329
Sc	11	23	11	10	11	8
Cu	21	173	38	142	45	122
Co	10	15	18	19	16	16
Zr	273	352	235	149	208	167
Y	28	34	32	21	29	23
Zn	70	114	117	81	93	84
Ni	48	53	77	69	67	57
Sr	814	1960	2022	213	1492	781
Rb	209	301	136	12	206	58
Cl	127	195	242	128	184	172
S	2277	147	97	41	379	136
Pb	18	19	13	8	89	12
CIPW Norms						
Q	21.99	7.93	—	0.39	—	—
Or	25.71	32.33	14.42	0.41	18.10	—
Ab	19.72	14.47	9.24	0.42	—	—
Ne	—	—	0.95	—	2.34	22.10
Ns	—	—	—	—	—	0.29
Lc	—	—	—	—	6.66	4.36
An	15.71	7.79	19.67	29.45	19.24	—
Di	3.74	29.56	25.12	24.46	23.04	27.64
Hy	7.65	—	—	—	—	—
Wo	—	2.98	25.92	37.55	23.11	42.09
Mt	0.99	0.81	0.14	1.62	2.52	—
Ilm	1.41	1.27	1.08	0.91	1.10	0.84
Ap	0.37	0.48	0.21	0.24	0.24	0.19
Ratios						
An	58	19	28	32	29	—
Di	14	73	36	27	35	40
Hy	28	—	—	—	—	—
Wo	—	7	37	41	35	60

Samples: 1, Calc-silicate hornfels (dark fraction) (NMV E10544) Blue Mt.; 2, Calc-silicate hornfels (pale fraction) (NMV E10544) Blue Mt.; 3, Calc-silicate hornfels (NMV E10280) Blue Mt.; 4, Calc-silicate hornfels (NMV E10283) Blue Mt.; 5, Calc-silicate hornfels (spotted) (NMV E10713) Blue Mt.; 6, Calc-silicate hornfels Bonnie Doon.

nd: not determined.

of calc-silicate hornfels from the Bonnie Doon location (Phillips & Wall 1980) was analysed. This specimen consisted mainly of wollastonite, diopside and K feldspar with small lenses of calcite, wollastonite and quartz. Major and trace element data are shown in Table 8.

The bulk rocks have variable composition, chiefly involving Ca and Si, and to a lesser extent K. Of the trace elements, Ba, Sr and S show the greatest variation. It is reasonable to assume that much of the chemical variation reflects differences in original sedimentary components, particularly in terms of the illite (clay-mica) (i.e. K), calcium carbonate (Ca) and quartz (Si) fractions. However, analyses of the dark and pale portions of sample E10544 indicate that alteration of the original dark hornfels resulted in the removal of Si, Al, Na and S and the concentration of Ca, K, Fe, Mg, Ba, Sr and Cl in the pale alteration zones. If this analysis pair is representative, then the metamorphism was not isochemical, at least in its final stages, but was accompanied by exchange of components from fluids in which Ca, Si, Na, S, Al and K were the most mobile elements. Thus any original compositional differences between individual rock types have been overprinted during metamorphism. The amount of chemical modification is difficult to quantify in the absence of clear zonation in assemblages. However, it is possible to derive a hypothetical reaction for the alteration of sample E10544 (neglecting oxidation of sulphides), based on the bulk rock compositions, the relative abundances of major minerals (Table 7), the average alkali feldspar composition in the dark fraction ($K_{0.5}Na_{0.4}Ca_{0.1}Al_{1.05}Si_{2.95}O_8$ —obtained by microprobe) and the average K-feldspar in the pale fraction ($K_{0.9}Na_{0.1}AlSi_3O_8$ —obtained by X-ray diffraction and microprobe):



This overall reaction does not quite balance, in that, as shown, it produces an extra 0.5 mole Cl^- , but this can be accounted for by the simplification of the feldspar compositions. The reaction results in the consumption of quartz and the production of diopside, in agreement with observed mineralogical changes during alteration (Table 7). All mobile cations (K, Ca, Mg, Fe, Si, Al, Na, H) are assumed to be present as chlorides, which is a further simplification, although chloride would have been a major component in the solutions (Vidale & Hewitt 1973). Note that the use of this equation implies that factors such as pH and the activities of silica, Ca^{2+} and Mg^{2+} may be of significance. A similar reaction could possibly be written involving plagioclase feldspars if compositions of reactants and products were known. Reaction 13 cannot account for the magnitude of the changes in bulk rock composition as alteration proceeded. However, if Al, Si and Na were removed in solution, and K and Ca added, the changes would be in the observed direction. The composition of each rock type in the (silica-saturated) Al_2SiO_5 —(Mg, Fe) SiO_3 — $CaSiO_3$ system is plotted in Fig. 13. The mineralogy

predicted from the plotted positions agrees well with that observed.

The widespread occurrence of grossular in the Blue Mount rocks, and its absence from the Bonnie Doon calc-silicates (where the equivalent assemblage plagioclase + wollastonite + calcite occurs—Phillips & Wall 1980) may arise from different Na contents in the bulk rocks. The progressive addition of albite to plagioclase solid solution results in a significant shift of the equilibrium (represented by reaction 10) with grossular formation being favoured by lower Na contents (Kerrick 1974).

CONDITIONS OF METAMORPHISM

Pressure and Temperature

There are no independent mineralogically-based means available to determine the pressure at which the Blue Mount rocks formed. However, some conclusions may be drawn from geological relationships. The granodiorite has intruded the main bounding fault of the Acheron cauldron complex, and hence largely postdates subsidence along the fault. From the nature of the emplacement mechanism of the volcanics, i.e. the filling of a collapse structure, it may reasonably be assumed that the levels of the top of the volcanic pile and the surrounding land surface outside the boundary fault were roughly concordant at the time of intrusion. The present altitude difference between the highest points on the eroded volcanic pile and Blue Mount is about 400 metres. Thus, if no more than 100 metres have been eroded from the vertical thickness of the volcanics, then the contact metamorphism could represent intrusion to depths as shallow as 500 metres. Even allowing for greater erosion rates, there is little doubt that the Blue Mount rocks crystallized at pressures of the order of 0.5 Kb or less. A similar conclusion was reached for the Bonnie Doon calc-silicate rocks (Phillips & Wall 1980).

Estimates of temperature may only be loosely based on the experimentally determined equilibria matching the natural assemblages (Fig. 12). The best reaction to constrain temperature is grossular + quartz \rightarrow 2 wollastonite + anorthite (9) since it is fluid-absent. Given that the calcic feldspar in the rocks is not pure anorthite, the estimated temperature from this equilibrium is a maximum. A maximum temperature of between 500° and 550°C is suggested for the Blue Mount rocks, in general agreement with estimates for the Bonnie Doon occurrence (Phillips & Wall 1980). Temperatures of around 400°C for equilibration in the retrogressive stages are suggested by the presence of vesuvianite, prehnite and scolecite.

Solution Chemistry

Binary solutions consisting of H_2O and CO_2 are the main agents involved in formation of calc-silicate assemblages under a wide range of conditions (Kerrick 1974, Rice & Ferry 1982). These solutions may be derived by either devolatilization reactions within the rocks during prograde metamorphism, or by infiltration of

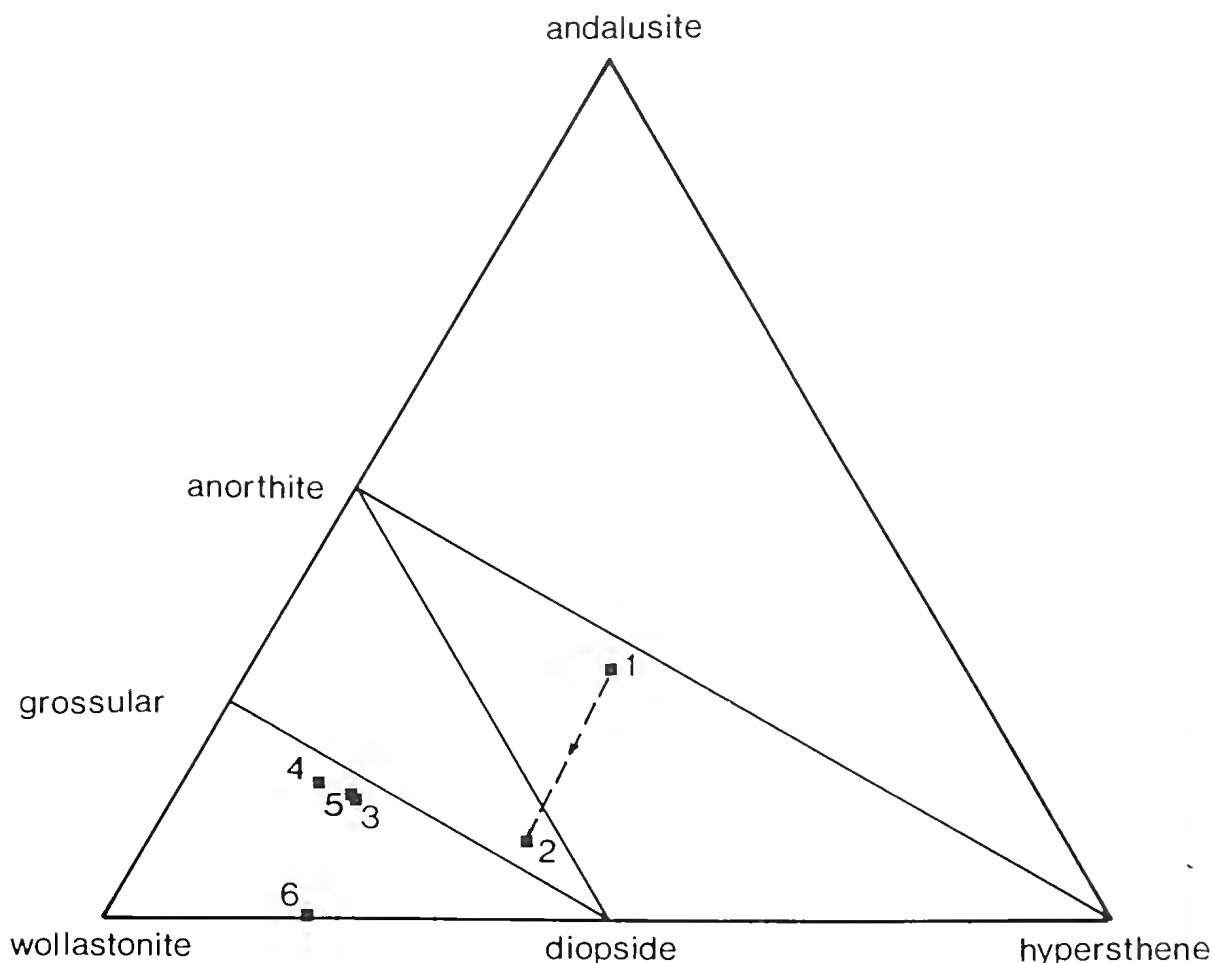


Fig. 13—Bulk compositions of the Blue Mount and Bonnie Doon calc-silicate rocks plotted in terms of normative components. The arrowed tie-line joins the dark and pale hornfels in sample E10544.

solutions from external sources, such as late-stage magmatic or meteoric fluids (Rumble *et al.* 1982). At Blue Mount, the main reactions (Fig. 12) occurring close to the peak of prograde metamorphism and responsible for the alteration of the dark hornfels are consistent with equilibration in the presence of solutions with X_{CO_2} less than 0.2. In some cases, particularly during crystallization of vesuvianite and prehnite during retrogression, extremely water-rich fluids ($X_{\text{CO}_2} < 0.05$) are indicated (Hochella *et al.* 1982, Williams-Jones 1981). Nearly all the devolatilization reactions occurring during progressive metamorphism of the Blue Mount rocks produced CO_2 . In order to maintain low X_{CO_2} , the CO_2 produced must have been diluted by a large reservoir of water-rich fluid, derived from either the intrusion, from the wet sediments themselves or from a meteoric source and transported along grain boundaries or on fracture systems. It is unlikely that the mixing process resulted in a totally homogenous fluid phase. The existence of coarse-grained patches, veinlets, clots, and remnant alteration textures in fine-grained rocks suggest

variable infiltration rates and hence variable fluid compositions. As an extreme example, the presence of both diopside-quartz and grossular-wollastonite veinlets, although not in the same rock type, represent the localized effects of CO_2 -rich and H_2O -rich solutions respectively. Phillips and Wall (1971) predicted variability of CO_2 activity on the scale of a handspecimen at Bonnie Doon, based on fluctuations in the proportions of coexisting wollastonite, calcite and quartz. Such an effect is likely in the Blue Mount rocks. In such a small-scale, unzoned deposit, across which P-T gradients may be undetectable, it is difficult to determine any mineralogical evidence for change in solution composition with time. However, it is likely that solutions became increasingly water-rich, resulting in localized crystallization of vesuvianite, prehnite and scolecite during retrogression.

The fluids responsible for the alteration of the dark hornfels were able to move significant amounts of Si, Al, Ca, Na, K, Cl and S through the Blue Mount rocks. These elements are likely to be amongst the most com-

mon and mobile in metamorphic fluids (Vidale & Hewitt 1973, Crawford *et al.* 1979, Ferry & Burt 1982, Ferry 1983). As well as cations, or cationic complexes, metamorphic fluids commonly contain significant H_2S , CH_4 (Ferry & Burt 1982), chlorides (Sisson *et al.* 1982, Crawford *et al.* 1979) and fluorides. Although the overall effect of up to 10 wt% NaCl on CO_2 activity in H_2O - CO_2 fluids may not be of significance at low pressures (Jacobs & Kerriek 1981), localized concentrations may influence the stable assemblage. For example, scapolite crystallization may occur in the presence of NaCl-rich fluids. Although fluorides are of lesser significance in metamorphic solutions, being strongly partitioned into crystallizing silicates, it is possible that localized F concentrations may favour formation of vesuvianite rather than grossular.

Apart from their ability to change the bulk chemistry of the rocks, the solutions influenced the structural state of the K feldspars. The slightly lower degree of order in the K feldspars from the pale altered zones compared to the dark hornfels suggests a higher crystallization temperature. However, it is unlikely that a significant temperature gradient could be maintained over such relatively short distances. As the continued presence of metamorphic solutions in the alteration zones would facilitate the K feldspar ordering process during cooling, the observed difference is the opposite to what might be expected. The explanation may lie in recrystallization during alteration which effectively removed pore fluids from the altered zones, so that the feldspar ordering process was not assisted. Alternatively compositional differences, particularly the higher levels of Ba in the altered zone K feldspars (small amounts of Ba may hinder ordering—Makagon & Schmakin 1971) may be sufficient to account for the structural state differences.

DISCUSSION AND CONCLUSIONS

Taylor and O'Neill (1977) defined skarn as referring to coarse-grained rocks which are the products of metasomatism, whereas calc-silicate hornfels best described rocks which are the result of isochemical metamorphism. This simple distinction has subsequently been recognised as inadequate to cover the diversity of skarn and skarn-like deposits (Einardi & Burt 1982). The contact metamorphism of the Blue Mount rocks was clearly not isochemical, at least on the scale of individual beds. The original sediments were a limited sequence of argillaceous limestones and calcareous mudstones. Metamorphism appears to have proceeded in two stages, particularly in the less reactive rock types represented by the dark hornfels. An early, largely isochemical (apart from devolatilization) recrystallization was followed by a later metasomatic alteration, the effects of which can only be monitored where the rocks were partially altered. In contrast to the dark hornfels, the massive pale hornfelsic and mottled rock types show no evidence for a multi-stage process. Local exchange of components between beds and partial homogenization, with the formation of 'skarnoids', have now been

recognised in interlayered sequences such as that on Blue Mount (Einardi & Burt 1982, Harris & Einardi 1982).

The fluids responsible for the metasomatism were either internally-derived from the presumably originally wet sediments themselves (i.e. they were a product of both pore fluids and devolatilization reactions) or else were of meteoric origin. Although the low-pressure, high-level environment may appear to favour the influx of magmatic fluids, the iron-rich assemblages characteristic of magmatic metasomatism are lacking in the carbonate rocks. Some magmatic influence cannot be ruled out entirely however, particularly if the overall system (intrusion plus sediments) was relatively depleted in iron.

The bulk chemistry of the rocks was variable, but within sufficiently narrow limits to enable the crystallization of grossular in most rock types. The overall low Na content was probably the critical factor influencing grossular crystallization.

Based on experimental and calculated data for relevant phase equilibria, the estimates for P-T conditions during metamorphism of the Blue Mount rocks ($P \leq 0.5$ Kb, $T_{max} = 500$ - $550^\circ C$) are in general agreement with those deduced for the only other stratigraphically similar occurrence in the region (Bonnie Doon). The major assemblages equilibrated in the presence of water-rich fluids ($X_{CO_2} < 0.2$).

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PROC. R. SOC. VICT. vol. 97, no. 1, 19-30, March 1985
STUDIES ON WESTERN AUSTRALIAN PERMIAN
BRACHIOPODS
5. THE FAMILY DICTYOCLOSTIDAE STEHLI 1954

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ABSTRACT: Dictyoclostidae from the Permian sequences of Western and northwestern Australia are revised and described. The new genus *Callytharrella* is diagnosed and the following species described: *Callytharrella callytharrensensis* (Prendergast), *Costiferina wadei* (Prendergast) and *Costiferina thomasi* sp. nov.

This paper continues the series of studies on Western Australian Permian brachiopods (Archbold 1984). Representatives of the Dictyoclostidae occur at selected stratigraphical horizons within the Permian sequences of the Perth, Carnarvon, Canning and Bonaparte Gulf Basins. The stratigraphy of these basins is documented in references referred to in Archbold (1981, p. 109) and the basis for age assignment of species is also outlined in Archbold (1981). Terminology is standard as in previous studies. Specimens are figured at natural scale in this study whereas previously (Prendergast 1943, Coleman 1957) important type and other specimens have been figured at reduced scales making comparisons with the other species and genera more difficult.

COLLECTIONS

All figured and measured specimens are housed in the following institutions as indicated by the prefix to the registered numbers. CPC—Commonwealth Palaeontological Collections of the Bureau of Mineral Resources, Geology and Geophysics, Canberra, A.C.T. GSWA—Geological Survey of Western Australia, Perth, Western Australia. MUGD—Department of Geology, University of Melbourne, Parkville, Victoria. UWA—Department of Geology, University of Western Australia, Nedlands, Western Australia. AMF—Australian Museum, Sydney, N.S.W.

SYSTEMATIC PALAEOLOGY

Order PRODUCTIDA Sarycheva & Sokolskaya 1959

Superfamily PRODUCTACEA Gray 1840

Family DICTYOCLOSTIDAE Stehli 1954

Genus *Callytharrella* gen. nov.

TYPE SPECIES: *Dictyoclostus callytharrensensis* Prendergast 1943.

DIAGNOSIS: Large, transverse dictyoclostids with large ears and ventral valve with broad, convex visceral disc and strongly curved, sulcate trail at maturity. No dorsal spines. Ventral spines scattered over visceral disc (associated with reticulate ornament), relatively few on long trail and small cluster on prominent ears. Costae prominent over anterior of ears at maturity and converge in sulcus. Dorsal valve strongly geniculate.

DISCUSSION: The examination of a large collection of specimens has permitted a substantial revision of Prendergast's *Dictyoclostus callytharrensensis*, as discussed below, which in turn has revealed the distinctive features of *Callytharrella* gen. nov. *Stereochia* Grant (1976) to which Prendergast's species was referred by Grant, and subsequently by Archbold (1982b), is distinguished from the new genus by means of its smaller quadrate ears with few spines, smaller size and less prominent trail. Mature *Callytharrella* gen. nov. is transverse whereas *Stereochia* is more quadrate in outline and the costae of *Callytharrella* gen. nov. are finer than those of *Stereochia*. Costae are distinct on the ears of gerontic *Callytharrella* gen. nov. but not on the ears of *Stereochia* where the costae are normally absent.

Other dictyoclostid genera are readily differentiated from *Callytharrella* gen. nov. *Costiferina* Muir-Wood and Cooper (1960) possesses a distinctive dorsal marginal ridge and its dorsal valve has a less extensive reticulate zone. Costae of *Callytharrella* gen. nov. are much finer than those of *Costiferina*. *Squamaria* Muir-Wood and Cooper (1960) is most readily distinguished from *Callytharrella* gen. nov. by the cluster of spines in 3 or 4 rows on the ventral ears as well as the cluster of spines on the dorsal ears. *Antiquatonia* Miloradovich (1945) is somewhat similar externally to *Callytharrella* gen. nov. however, differs in possessing rare dorsal spines and a distinctive curved row of spines on the ventral flanks, often developed on a distinct rounded ridge. Costae of *Antiquatonia* are finer than those of *Callytharrella* gen. nov. *Reticulatia* Muir-Wood and Cooper (1960) resembles *Callytharrella* gen. nov. externally but *Reticulatia* possesses a weakly developed sulcus and few, fine ventral spines. *Reticulatia* also possesses a distinct dorsal marginal ridge and distinctive overlapping growth lamellae on the anterior of the ventral valve. Costae are poorly developed or absent on the ears of *Reticulatia*.

Callytharrella callytharrensensis (Prendergast, 1943)
Figs 1A-T, 2A-F, 3A-H

1902 *Productus semireticulatus*: Etheridge. In, Maitland, A.G.; *Ann. Prog. Rep. Geol. Surv. W. Aust.*, 1901: 12.

- 1903 *Productus semireticulatus*: Maitland. In, Fraser, M.A.C. (ed.); *Notes on the Natural History etc. of Western Australia*, p. iv.
- 1903 *Productus semireticulatus*: Etheridge. *Bull. geol. Surv. W. Aust.*, 10: 18, pl. 2, figs 3-5.
- 1904 *Productus semireticulatus*: Maitland. *Rep. A'sian Assoc. Advmt Sci.*, 10: 619.
- 1907 *Productus semireticulatus*: Etheridge. *Bull. geol. Surv. W. Aust.*, 27: 29.
- 1910 *Productus semireticulatus*: Gläuert. *Bull. geol. Surv. W. Aust.*, 36: 87.
- 1912 *Productus semireticulatus*: Maitland. *Jour. Nat. Hist. Sci. Soc. W. Aust.*, 4: 23, 26.
- 1919 *Productus semireticulatus*: Maitland. *Mem. geol. Surv. W. Aust.*, 1: 34, 38.
- 1924 *Productus semireticulatus*: Chapman. p. 36.
- 1931 *Productus semireticulatus*: Hosking. *J. Roy. Soc. W. Aust.*, 27: 8, 22.
- 1936 *Productus semireticulatus*: Chapman. In, Raggatt, H. G., *J. Proc. Roy. Soc. N.S.W.*, 70: 128.
- 1937 *Productus semireticulatus*: Clarke. *Rep. Aust. N.Z. Assoc. Advmt Sci.*, 24: 429.
- 1937 *Productus semireticulatus*: Raggatt and Fletcher. *Rec. Aust. Mus.*, 20(2): 168, 169, 174.
- 1937 *Productus cf. spiralis*: Raggatt and Fletcher. *Rec. Aust. Mus.*, 20(2): 169, 174.
- 1937 *Productus cf. indicus*: Raggatt and Fletcher. *Rec. Aust. Mus.*, 20(2): 169, 174.
- 1943 *Dictyoclostus callytharrens* Prendergast, p. 13, pl. 1, figs 1-7; pl. 2, fig. 1.
- 1943 *Dictyoclostus spiralis*: Prendergast, p. 18, pl. 2, figs 8-9.
- 1952 *Dictyoclostus callytharrens* Prendergast: Teichert. *Symposium sur les Series de Gondwana; 19th Int. Geol. Cong. Alger*, pp. 117, 121, 122.
- 1957 *Dictyoclostus* (?*Antiquatonia*) *callytharrens* Prendergast; Coleman, p. 54, pl. 6, figs 3-14.
- 1957 *Dictyoclostus* (?*Antiquatonia*) *magnus* Coleman, p. 57, pl. 7, figs 1-6.
- 1967 *Dictyoclostus callytharrens* Prendergast; Condon, p. 70.
- 1967 *Dictyoclostus magnus* Coleman; Condon, p. 70.
- 1967 *Dictyoclostus* Condon, p. 90.
- 1969 *Costiferina callytharrens* (Prendergast); Thomas. In, *Gondwana Stratigraphy (I.U.G.S. Symp.)*, p. 220.
- 1971 *Reticulatia callytharrens* (Prendergast); Waterhouse. *Proc. Pap. 2nd Gondwana Symp.*, p. 391.
- 1971 ?*Reticulatia magnus* (Coleman); Waterhouse. *Proc. Pap. 2nd Gondwana Symp.*, p. 391.
- 1975 *Dictyoclostus callytharrens* Prendergast; Playford *et al.*, pp. 233, 281, 282.
- 1976 *Costiferina callytharrens* (Prendergast); Playford *et al.*, p. 95.
- 1976 *Costiferina magnus* (Coleman); Playford *et al.*, p. 95.

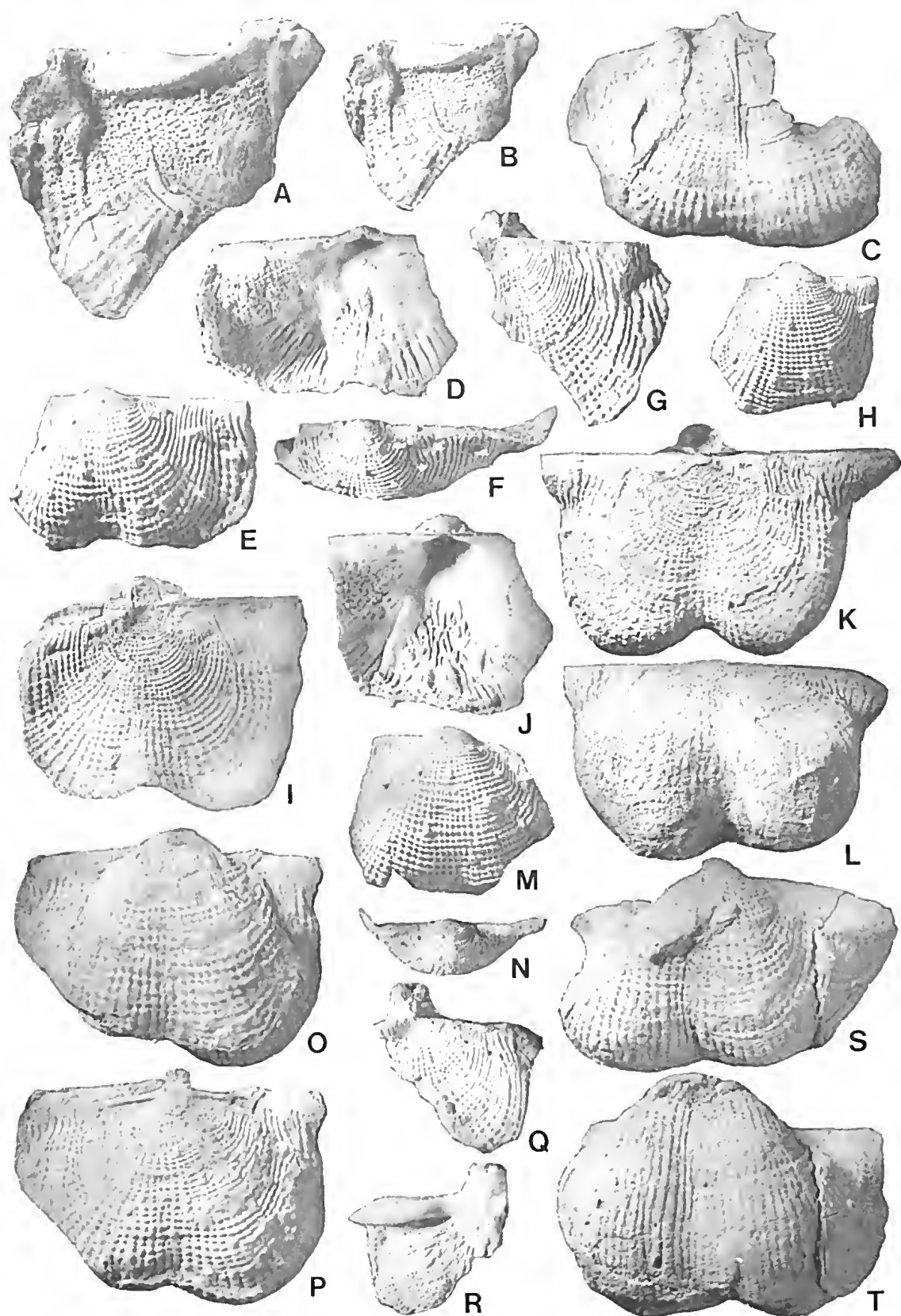
LECTOTYPE: GSWA 1/4967b figured by Prendergast (1943, pl. 1, fig. 3) and Coleman (1957, pl. 6, figs 9, 10); 0.8 km west of Callytharra Springs, Wooramel River District, Callytharra Formation, chosen by Coleman (1957, p. 54).

MATERIAL, LOCALITIES AND AGE: Specimens as figured and measured in addition to abundant, usually crushed and incomplete material from the Callytharra Formation in the GSWA and MUGD collections include: AMF 36514 and AMF 36515, 2 ventral valves from Wyndham Gap, Callytharra Formation, Carnarvon Basin. MUGD F 6006-6007, 2 incomplete ventral valves from locality P 494; F 6008, an incomplete ventral valve from locality P 481; F 6013-6114, an incomplete dorsal valve and a ventral valve from locality P 498, all G. A. Thomas localities, type section of Callytharra Formation, Callytharra Springs; 34 m, 29 m, 24 m and 34-38 m from base of formation respectively. MUGD F 6018-6019, a ventral valve and an incomplete shell from G. A. Thomas locality R 654, in ridge on north side of Baragooda Pool, Arthur River, Bidgemia Station, 30.15 m above base of measured section of Callytharra Formation. MUGD F 6020-6021, a dorsal valve external mould and an incomplete dorsal valve from G. A. Thomas locality S665, 8.4 km bearing 226° from Coondoo Outcamp, Bidgemia Station near base of Callytharra Formation. CPC 19910, a ventral valve BMR locality GW 134, 25°52'S, 115°31'E, type section of Callytharra Formation, Callytharra Springs, 27-32 m above base of formation. All Sterlitamakian (Late Sakmarian).

GSWA F 270, a conjoined shell and GSWA F 6380, a ventral valve both from Fossil Cliff, Irwin River District, type section of Fossil Cliff Member, Perth Basin. Sterlitamakian (Late Sakmarian).

CPC 19911, a conjoined shell from BMR locality WO3, type section of the Jimba Jimba Calcarenite (25°02'75"S, 114°58'5"E), Jimba Jimba Station, 15 km west of Jimba Jimba Homestead (Condon 1967, p. 89) Carnarvon Basin. Aktastinian (Early Artinskian).

Fig. 1—A-T, *Callytharrella callytharrens* (Prendergast). A-N, Q-R, from Callytharra Formation, Carnarvon Basin; O-P, S-T, from Fossil Cliff Member, Perth Basin. A,B,G, MUGD F6012, incomplete dorsal valve in ventral views, $\times 2$ and $\times 1.1$ and dorsal view, $\times 1.1$. C, MUGD F6013, incomplete dorsal valve in ventral view, $\times 1$. D-F, MUGD F6008, incomplete ventral valve in dorsal, ventral and posterior views, $\times 1.3$, $\times 1.3$ and $\times 1.6$ respectively. H, J, MUGD F6006, incomplete ventral valve in ventral and dorsal views, $\times 1.3$ and $\times 2$ respectively. I, MUGD F6019, incomplete shell in dorsal view, $\times 1$. K,L, MUGD F6020, dorsal valve external mould in ventral and anterior views, $\times 1$. M,N, MUGD F6007, incomplete ventral valve in ventral and posterior views $\times 1$. O-P, GSWA F270, shell in ventral view and corresponding dorsal valve, $\times 1$. Q-R, MUGD F6011, incomplete dorsal valve in dorsal and ventral views, $\times 2$. S-T, GSWA F6380, ventral valve in posterior and ventral views, $\times 1$.



MEASUREMENTS (in mm): e = estimate

Specimen	Hinge width	Mid-length width	Ventral height	Dorsal height	Thickness	Formation
AMF 36514	86	80	51	—	43e	Callytharra
AMF 36515	61+	51e	—	—	—	Callytharra
MUGD 6010	58e	50e	45	—	30e	Callytharra
MUGD 6018	74	58e	49e	—	—	Callytharra
CPC 19911	51+	51	52	41	40	Jimba
						Jimba
GSWA F 270	40+	45	35	32	—	Fossil Cliff
GSWA F 6380	48e	48e	41e	—	—	Fossil Cliff

DIAGNOSIS: Huge for genus. Ornamentation fine for size of species; ears distinct. Costae grouped into weak fasciculae on weak folds of trail. Ventral sulcus distinct, dorsal fold developed anteriorly.

DESCRIPTION: Huge for genus; outline transverse, widest at hinge at maturity; profile fairly evenly curved, gentle geniculation at anterior of visceral disc. Ears inflated, distinctly alate in gerontic individuals, tips of ears squared presenting quadrate outline. Anterior margin emarginate producing broad, deep sulcus. Ventral umbo short, slightly inflated; visceral disc strongly reticulate. Rugae initially stronger than costae (for first cm of growth) then costae of equal strength; costae continue forward of rugae for anterior two-thirds of fully mature shells; costae strong, fine (0.5 to 1.5 mm wide on trail), crests rounded, occasionally bifurcating on the anterior side of spine, superimposed on weak raised folds (or plications) of shell, group of three or four fine costae arise on each plication, this pattern imparting weak fasciculate appearance to costae on trail; costae persist to anterior of trail. Costae converge in sulcus, at least one pair being lost. Sulcus arises about midpoint of visceral disc, indistinct initially. Spines prominent, in row parallel to hinge with minute spines near umbo and up to seven coarse spines on ears of gerontic individuals, including about four in row near hinge, widely spaced row near depression demarcating ears from rest of ventral valve each progressively coarser with the final two spines of row functional, finer spines scattered over visceral disc usually abraded off mature specimens, coarser spines scattered at random on trail—about 10 functional; diameter of anterior trail spines 1.5 to 2 mm. Dorsal valve slightly concave on visceral region with low median fold; strongly geniculated to form trail; body chamber large; reticulate ornament extends over entire visceral disc; trail costate as on ventral valve; no spines; low pits scattered over valve, broadly corresponding to ventral spine positions. Hinge edge sharp, bearing against low, distinct ventral ginglymus.

Ventral interior deep, pitted visceral region (excluding muscle scars); diductor scars large, longitudinally striate; adductor scars dendritic, narrow, anteriorly on slightly raised median platform; exterior ornament weakly reflected on inner surface of valve ex-

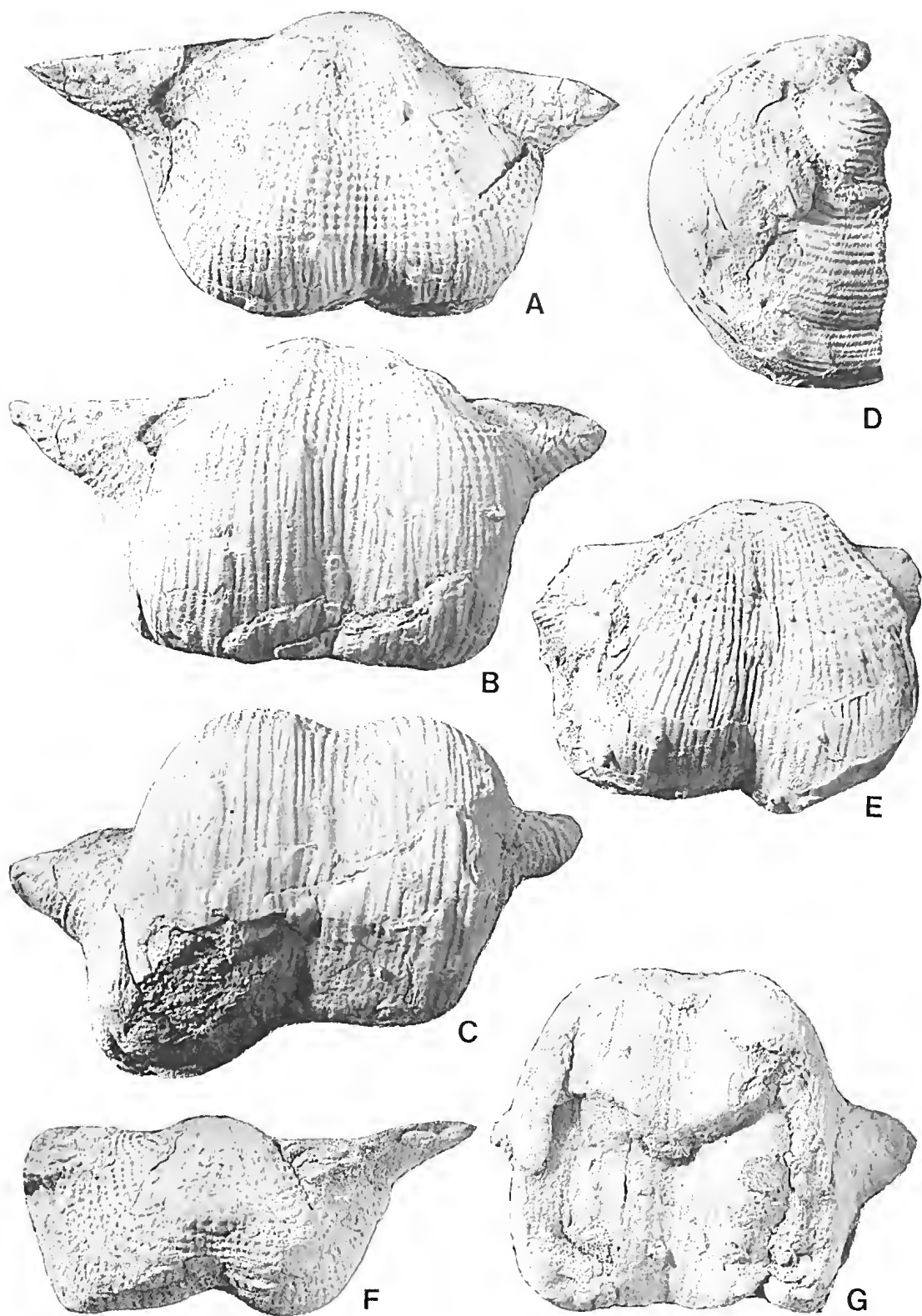
cept where thickened or scarred. Ginglymus possesses small V-shaped notch under umbo in juvenile shells, subsequently sealed by shell thickening. Dorsal interior with low marginal ridge across ears, absent anteriorly; cardinal process short, trilobed, with small, sharp lophidium not continuous with median myophore; median lobe reduced in thickened specimens; process supported by lateral ridges and median septum which continues forward between muscle scars becoming thinner and sharper, terminating about two-thirds distance to geniculation. Adductor scars in two pairs, median pair extending forward further than lateral pair; brachial ridges weak to distinct, tear-shaped anteriorly.

DISCUSSION: *Callytharrella callytharrens*, although a common species, is invariably represented by incomplete, crushed specimens normally with the ears damaged and the trail broken and crushed or completely removed. Specimens examined for the present review permit a uniting of the two species *Dictyoclostus callytharrens* Prendergast and *Dictyoclostus* (?*Antiquatonia*) *magnus* Coleman. The holotype of Coleman's species is a gerontic representative of Prendergast's species and the differences between the two species, as discussed by Coleman (1957, p. 58), can be explained by ontogenetic variation. The older the individual, the smaller the proportion of the shell which possesses reticulate ornament so that mature specimens of *C. callytharrens* possess reticulate ornament for about one-third of the curvilinear length of the ventral valve. The spiral ornament of the costae on the ears of "*Dictyoclostus magnus*" is also a result of ontogenetic change; the ears of mature *C. callytharrens* curl and the incipient costae, mentioned by Prendergast (1943, p. 14) become more strongly developed and appear to spiral or curl around them. The costae in the sulcus also appear to converge into the sulcus only at maturity and hence young specimens of *C. callytharrens* [as documented by Prendergast (1943) and Coleman (1957)] lack that ornamental feature. As the two species, *D. callytharrens* and *D. magnus*, have been quoted widely in the literature a full synonymy is given above. Chapman's report (1924a) is retained in the synonymy following Prendergast (1943, p. 13); this would imply that *C. callytharrens* is present in the Canning Basin (probably the Nura Nura Member) as shown by Coleman (pp. 137-139) but this has not been verified by the present review.

The Western Tibetan, early Artinskian species, *Costiferina sinensis* Sun (1983, p. 125, pl. 16, figs 8-10), a smaller species than *C. callytharrens*, possesses external ornament similar to that of the Western Australian species. The sulcus of the Tibetan species is narrow and the ears poorly known but *C. sinensis* is provisionally assigned to *Callytharrella*.

Several other large Permian dictyoclostids may be

Fig. 2—A-G, *Callytharrella callytharrens* (Prendergast). A-G, from Callytharra Formation, Carnarvon Basin. A-D, AMF 36514, gerontic ventral valve in posteroventral, ventral, anterior and lateral views, $\times 1$ (the holotype of *Dictyoclostus magnus* Coleman 1957). E, MUGD F6014, ventral valve in ventral view, $\times 1$. F-G, AMF 36515, ventral valve in posterior and ventral views, $\times 1$.



related to *C. callytharrens* but comparisons with reports and illustrations are usually hampered by the incomplete nature of the material described or figured. *Productus semireticulatus* of Broili (1916, pl. 2, fig. 14) from Sonnebekoe, Timor of "Bitauini" age approaches *C. callytharrens* in terms of size but has a less well developed sulcus, smaller ears and finer spines. *Productus spiralis* of Broili (1915, pl. 21, figs 7-9) from a "Bitauini" fauna of Letti is very close to juvenile and sub-mature *C. callytharrens* in terms of ventral valve outline, dorsal valve geniculation and external ornament. Ontogeny of the Letti species is unknown. *Productus uralicus* Tschernyschew (1902, pl. 32, fig. 1; pl. 33, fig. 1; pl. 62, fig. 1) from the Sakmarian of the Urals is a large species with large ears—without well developed costae—and incipient bundling of the anterior ventral costae, but the finer ornament, particularly that of the dorsal valve recalls *Reticulatia* to which Sarycheva (1977) referred the species. Specimens referred to *Productus uralensis* Liehew by Ustritskiy (1960, pl. 9, figs 3, 4; pl. 10, figs 1-4) from the Sakmarian of the Kun Lun Mountains, China are closer to *C. callytharrens* in terms of size, ventral sulcus, ornament and ears although costae are not as distinctive on the ventral ears. *Stereochia koyaoensis* Waterhouse (1981) from the Late Sakmarian or Early Artinskian of southern Thailand, is not as large as *C. callytharrens*, and can be distinguished by means of its coarser costae and smaller ears (Waterhouse 1981, p. 85). *Productus spiralis* Waagen (1884, p. 681; pl. 67, fig. 6; pl. 68, fig. 3) from the Amb Formation of the Salt Range, with which large specimens of *C. callytharrens* had previously been compared, is a large form that may be allied to *Callytharella*, but judging from Waagen's illustrations, the ventral reticulate ornament is restricted to about one-fifth of the curvilinear height and the ears are essentially smooth except for a few spines.

Genus *Costiferina* Muir-Wood & Cooper 1960

TYPE SPECIES: *Productus indicus* Waagen 1884.

DIAGNOSIS: The diagnosis provided by Muir-Wood and Cooper (1960, p. 277) is accepted.

DISCUSSION: *Costiferina wadei* (Prendergast 1943) is referred herein to *Costiferina* on the basis of its coarse ornament of costae and less extensive reticulate zone. Nevertheless the dorsal interior of the species is poorly known and an absence of a prominent dorsal marginal ridge may permit assignment of the species to *Stereochia* as in Archbold (1982b).

Costiferina wadei (Prendergast 1943)

Fig. 4A-L

1937 *Productus semireticularis*: Wade. Rep. Aust. N.Z. Assoc. Advmt. Sci., 23: 94.

1943 *Dictyoclostus callytharrens* var. *wadei* Prendergast, p. 16, pl. 1, figs 2-4.

Fig. 3—A-H, *Callytharella callytharrens* (Prendergast). A-E, from Jimba Jimba Calcarenite, Carnarvon Basin; F-H, from Callytharra Formation, Carnarvon Basin. A-E, CPC 19911, shell with ears missing in posterior, dorsal, ventral, anterior and lateral views, $\times 1$. F, CPC 19910, ventral valve in ventral view, $\times 1$. G, MUGD F6021, incomplete dorsal valve in ventral view, $\times 1$. H, MUGD F6018, ventral valve in ventral view, $\times 1$.

1957 *Dictyoclostus wadei* Prendergast; Coleman, p. 59, pl. 7, figs 7-10.

1958 *Dictyoclostus wadei* Prendergast; Guppy et al. Bull. Bur. Min. Res. Geol. Geophys., 36: 48.

1971 *Costiferina wadei* (Prendergast); Waterhouse. Proc. Pap. 2nd Gondwana Symp., p. 391.

1975 *Dictyoclostus wadei* Prendergast; Playford et al., p. 341.

HOLOTYPE: UWA 20453 from ferruginous limestone, 3.2 km east, 10 degrees south of Mount Nicholson, West Kimberley District, from lower half of Noonkanbah Formation.

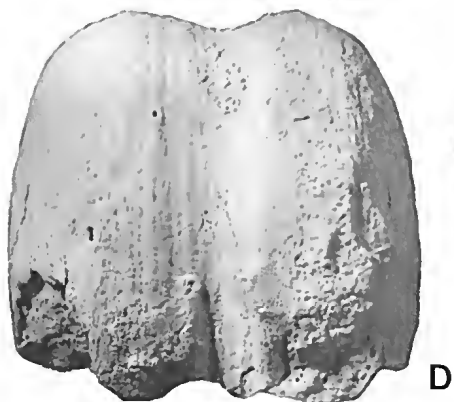
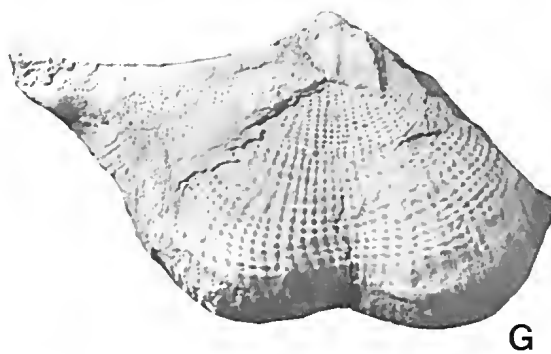
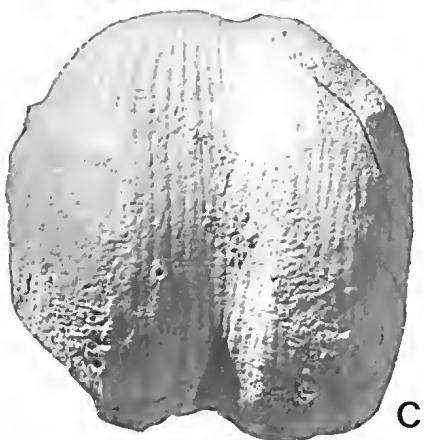
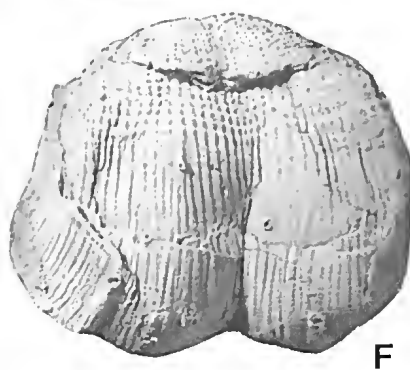
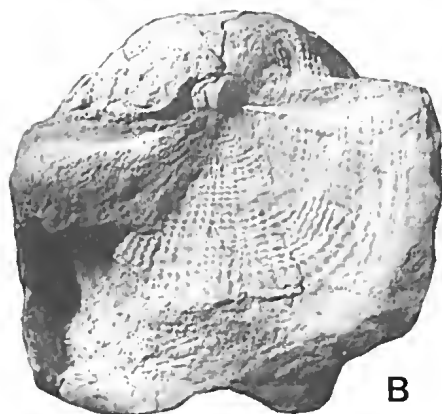
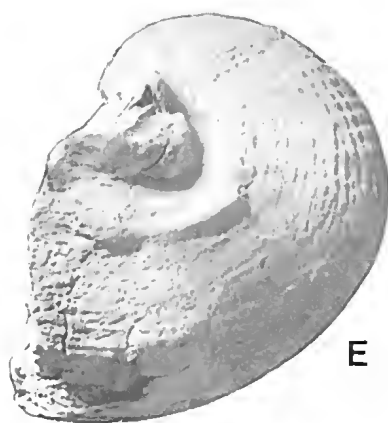
MATERIAL, LOCALITIES AND AGE: Specimens examined by Coleman (1957) and re-examined—see Coleman for localities. In addition, CPC 19912-19914, 2 ventral valves and 1 dorsal valve and several fragments, all from BMR locality KNA 20, about 13 km bearing 120° from Mount Anderson Homestead, west Kimberley Division, about 180 m above base of measured section, south of Grant Range, Noonkanbah Formation, Canning Basin were examined. Late Baigendzinian (Late Artinskian).

MEASUREMENTS (in mm): * = holotype e = estimate

Specimen	Hinge width	Midlength width	Ventral height	Dorsal height	Thickness
CPC 19912	60e	46	47	—	31
CPC 19913	46	44	—	—	—
CPC 19914	—	41	—	36 +	—
UWA 20453*	63	50	54	—	35
UWA 28696b	37	33	—	22	—

DIAGNOSIS: Average sized for genus with coarse ornamentation. Ears large, quadrate. Costae broad, bifurcating anteriorly of spines. Sulcus distinct, dorsal fold distinct.

DESCRIPTION: Average to large size for genus; outline transverse, widest at hinge at maturity; profile evenly curved; ventral geniculation not pronounced. Ears distinct, quadrate in outline, separated from flanks of ventral valve by low depression at maturity. Anterior margin emarginate producing broad, relatively deep sulcus. Ventral umbo short; visceral disc strongly reticulate, rugae at times particularly strong, sulcus arises within first centimetre of umbo. Costae continue forward of rugae for anterior two-thirds of fully mature shells. Costae strong, coarse (1 to 3 mm wide on trail), crests rounded, occasionally bifurcating—normally on anterior side of spine; costae persist to anterior of trail, converge slightly in sulcus—one or two may be lost. Spines coarse, two large and several smaller spines on ears, two or three coarse spines on flanks close to depression separating ears. Spines scattered at random on trail, about eight functional; diameter of anterior trail spines 2.2 to 3.1 mm on CPC 19912. Dorsal valve visceral disc gently concave, median fold arises within first centimetre of growth. Reticulation strong, especially rugae, no spines but with occasional pits. Hinge edge sharp.



Ventral interior poorly known except for normally shaped, longitudinally striate, diductor muscle scars. Dorsal valve with short, trilobed, robust cardinal process supported by strong lateral ridges.

Discussion: Old reports of collections from the Canning Basin that may indicate this species, under the name *Productus semireticulatus*, are those of Hardman (1885, p. 26) and Chapman (1924b, p. 19; 1925, p. 6). *Costiferina wadei* is now well known except for details of the dorsal interior. Coleman (1957, p. 59) noted that the dorsal interior features of *C. wadei* are similar to those of *Callytharrella callytharrensensis* except that "the dendritic adductor muscle impressions are set closer to the hinge-line". The available information on the morphology of the species strongly supports its assignment to *Costiferina*. Although *C. wadei* was compared with *Stereochia* by Grant (1976) and Archbold (1982b), the coarse ventral costae strongly recall those of *Costiferina* and hence permit a more restricted diagnosis for *Stereochia* with only *S. liostyla* Grant (1976) and *S. irianensis* Archbold (1982b) being reliably attributed to that genus.

Typical species of *Costiferina* with coarse ventral costae such as *C. indica* Waagen and *C. vishnu* Waagen as figured by Muir-Wood and Cooper (1960, pl. 95, figs 6-7; pl. 103, figs 1-12) differ from *C. wadei* in possessing somewhat shallower sulci and *C. vishnu* possesses much weaker dorsal reticulate ornament and reduced ventral ornament anteriorly. *Costiferina indica* Waagen (1884, pl. 70, figs 1-6) from a variety of horizons in the Middle and Upper Productus Limestones of the Salt Range is closest to *C. wadei* but differs in its generally smaller size and normally less prominent ears. *Costiferina alata* Waterhouse (1966) is a much larger species with alate ears and comes from Chhidruan strata of Nepal (see also Waterhouse 1978a, pl. 2, figs 21, 22; pl. 3, figs 1-5) Kashmir (Waterhouse & Gupta 1979, pl. 4, figs 1-3) and Tibet (Chang & Ching 1976, pl. 6, figs 1-10). Specimens from the Chhidruan of Tibet illustrated by Ting (1962, pl. 3, fig 3a-d) and attributed to Waterhouse's species by Chang and Ching (1976) possess broad dorsal costae that dominate the dorsal reticulate ornament much as in the dorsal ornament of *C. wadei*. *Costiferina miaolingensis* Lec and Gu (1980, in Lec *et al.* 1980) from the Late Early Permian of Inner Mongolia is also a transverse form with wide ears and costae finer than those of *C. wadei*.

Although referred to *Tyloplecta* by Muir-Wood and Cooper (1960), *Productus sumatrensis* Roemer (1880, pl. 1, fig 4a-b; specimen refigured more accurately by Fliegel 1901, pl. 6, figs 1a-c) from the Kungurian of Sumatra appears to be a *Costiferina* and is close to *C. wadei* in details of size and ventral sulcus but the costae of *C? sumatrensis* do not appear to converge in the

sulcus. The dorsal valve reticulate ornament of *C? sumatrensis* (see Meyer, 1922, pl. 2, fig. 5a) is similar to that of *C. wadei*.

Costiferina thomasi sp. nov.

Fig. 5A-K

1957 *Dictyoclostus* sp. Thomas, p. 181.

1958 *Dictyoclostus* sp. Thomas, *Abstracts ANZAS 1958, Sec. C*, p. 3

1969 *Costiferina* sp. nov. Thomas, p. 221

ETYMOLOGY: For Dr G. A. Thomas, collector of the species.

HOLOTYPE: CPC 24332, an external mould of a dorsal valve from the Upper Marine Beds, Port Keats Group, Bonaparte Gulf Basin.

MATERIAL, LOCALITIES AND AGE: CPC 24332-24334, one dorsal valve external mould (holotype), one incomplete dorsal valve external mould and one incomplete dorsal valve internal mould, all from G. A. Thomas locality PK4, on coast approximately 13.5 km north of Cape Dombey, Port Keats Arca, Northern Territory, Upper Marine Beds, Port Keats Group. CPC 24335-24337, one internal mould of a ventral valve, one incomplete external mould of a dorsal valve and one natural cast of a fragment of a dorsal valve, all from G. A. Thomas locality PK1, Tchindi Beach, approximately 15 km west of Port Keats Mission, Northern Territory, Upper Marine Beds, Port Keats Group, Bonaparte Gulf Basin (see Thomas 1957, p. 176 for map of localities). Chhidruan.

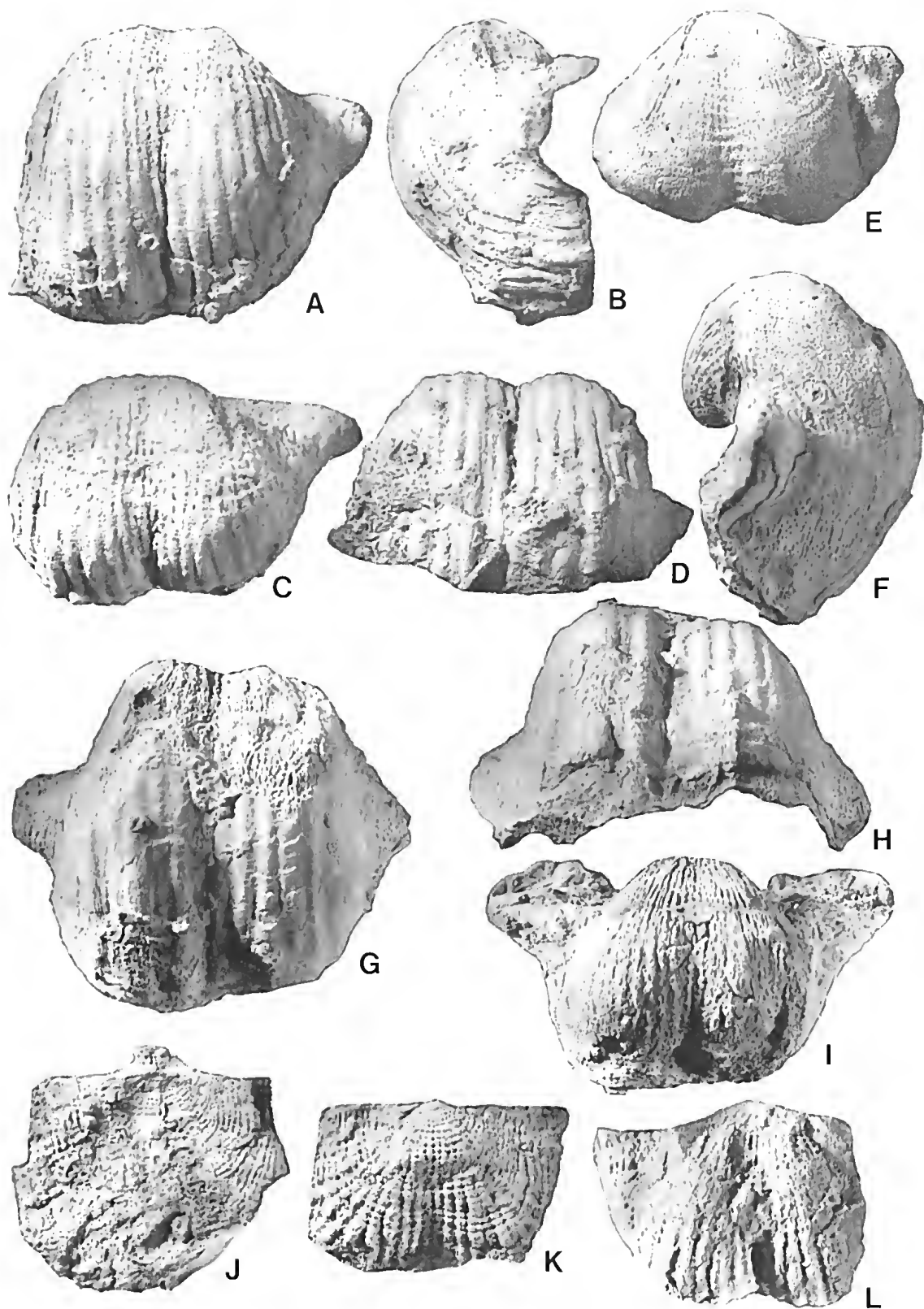
MEASUREMENTS (in mm): * = holotype, c = estimate

Specimen number	Hinge width	Midlength width	Ventral height	Dorsal height
CPC 24332*	58	47e	—	39
CPC 24333	82e	66e	—	43
CPC 24334	—	66 +	—	46
CPC 24335	68	61	54	—
CPC 24336	72e	60e	—	45e
CPC 24337	—	—	—	38

DIAGNOSIS: Moderately large for genus. Well developed reticulate ornament on dorsal visceral disc. Costae on trail relatively fine for genus. Dorsal fold well developed on trail. Ears prominent on mature specimens.

DESCRIPTION: Moderately large for genus; outline transverse, widest at hinge at maturity. Ventral geniculation distinct, dorsal geniculation sharp, turning through 90°. Ears subquadrate at submaturity, distinctly alate in mature specimens. Anterior margin emarginate producing relatively broad, shallow sulcus. Ventral umbo low. Ventral exterior ornament poorly known. Anterior of ventral valve preserved on CPC 24336 reveals strong costae varying from 2.0 to 2.8 mm wide with rounded crests. Spines distinct on trail but few in number, scattered randomly; spine bases about 2 mm in diameter.

Fig. 4—A-L, *Costiferina wadei* (Prendergast). A-L, from Noonkanbah Formation, Canning Basin. A-D, CPC 19912, ventral valve in ventral, lateral, posterior and anterior views, $\times 1$. E, CPC 19913, worn ventral valve in ventral view, $\times 1$. F-I, holotype, UWA 20453, ventral valve in lateral, ventral, anterior and posterior views, $\times 1$. J, CPC 19914, dorsal valve in dorsal view, $\times 1$. K, UWA 28696b, external mould of dorsal valve, $\times 1$. L, UWA 28696a, incomplete ventral valve in ventral view, $\times 1$.



Ventral sulcus only weakly developed on trail. Dorsal valve with gently concave visceral disc with low median fold arising within 2 cm of umbo. Fold more pronounced on trail of dorsal valve. Reticulate ornament extends over entire visceral disc with costae becoming dominant at anterior of disc and rugae being absent on trail. Size of visceral disc varies greatly between individuals indicating considerable size variation within species. Trail strongly costate, costae ranging from 1.5 to 3.0 mm wide. No dorsal spines but abundant low, elongate shallow pits scattered over visceral disc—probably reflecting the ventral spine positions. Hinge edge sharp. Ventral interior moderately deep with large diductor scars, longitudinally striated. Exterior ornament not reflected on interior of ventral visceral disc. Dorsal interior with broad marginal ridge across ears, apparently continuing anteriorly around visceral disc; cardinal process large, trilobed with prominent median lobe. Process supported by lateral ridges and median septum which continues forward between muscle scars, terminating about two-thirds distance to geniculation. Adductor scars in two pairs, median pair extending forward further than lateral pair; brachial ridges relatively weak, tear-shaped anteriorly. Dorsal exterior reticulate ornament reflected weakly on anterior of visceral disc.

DISCUSSION: *Costiferina thomasi* sp. nov. remains imperfectly known in terms of ventral exterior and full details of the dorsal interior. It appears to be a variable species and large collections are required to assess this. However the material is distinctive and hence is formally named.

Costiferina wadei is distinguished from the new species by its coarser ventral spines and coarser costae on its trail. Dorsal valve costae towards the anterior of the visceral disc on *C. wadei* are also much coarser than those of *C. thomasi*. *Costiferina alata* Waterhouse (1966) approaches *C. thomasi* sp. nov. with its alate ears in mature individuals but is a larger species and possesses much coarser costae over the dorsal visceral disc. The dorsal exterior figured by Waterhouse (1978, pl. 2, fig. 21) from the Chhidruan of Nepal approaches that of *C. thomasi* sp. nov. and indicates that *C. alata* can possess finer dorsal ornament. Of Waagen's (1884) species attributed to *Costiferina*, *C. indica* possesses much coarser costae on the ventral trail and is a smaller species with less alate ears. *C. vishnu* possesses weakly developed dorsal reticulate ornament and anterior ventral costae.

The Basleo specimens referred to *Productus spiralis* by Broili (1916, pl. 3, figs 3, 4) appear to be close to *C. thomasi* sp. nov. because their costae are relatively fine for *Costiferina* and the zone of reticulate ornament is moderately extensive. *Costiferina* spp. figured by

Shimizu (1981, pl. 7, figs 15-19) from various late Permian units of Kashmir, although poorly known, are noteworthy because of their extensive dorsal reticulate ornament, hence recalling *C. thomasi* sp. nov.

ACKNOWLEDGEMENTS

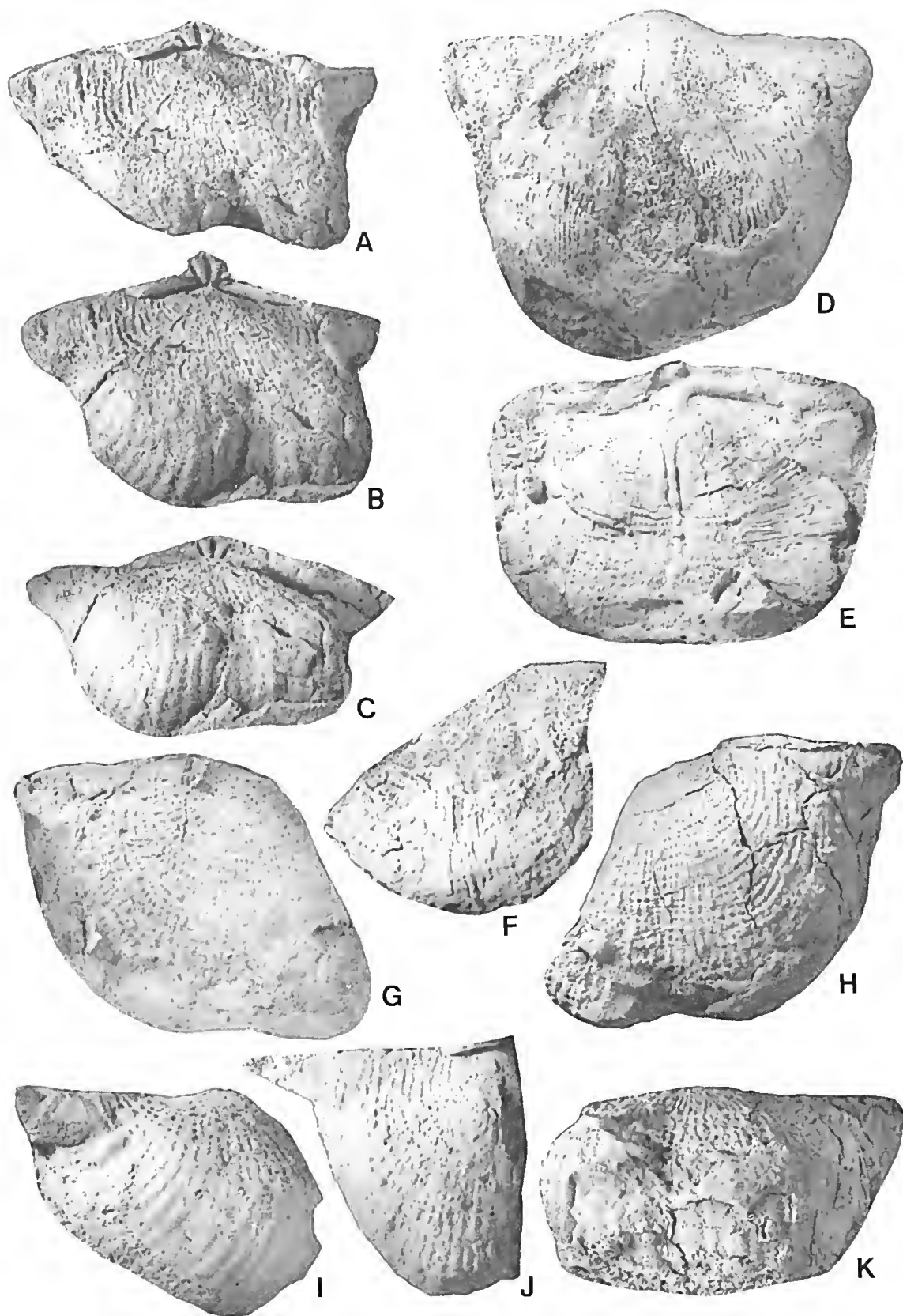
Dr J. M. Dickins, Bureau of Mineral Resources, Geology and Geophysics; Dr A. E. Cockbain, Geological Survey of Western Australia; Mr D. Rhodes, Department of Geology, University of Western Australia; Dr A. Ritchie, the Australian Museum and Dr G. A. Thomas, Department of Geology, University of Melbourne are all thanked for the loan of specimens.

Dr G. A. Thomas read an earlier version of the manuscript and Mrs I. Munro typed the manuscript.

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Fig. 5—A-K, *Costiferina thomasi* sp. nov. A-K, from Upper Marine Beds, Port Keats Group, Bonaparte Gulf Basin. A-C, holotype, CPC 24332, dorsal valve external mould in three views, progressively tilted, $\times 1$. D, CPC 24335, ventral valve internal mould in ventral view, $\times 1$. E, CPC 24334, latex replica of dorsal valve internal mould, $\times 1$. F, CPC 24337, natural cast of fragment of dorsal valve interior, $\times 1$. G, H, K, CPC 24336, latex replica of dorsal valve external mould and dorsal valve external mould in direct and anterior views, $\times 1$. I, J, CPC 24333, incomplete dorsal valve external mould in lateral and direct views, $\times 1$.



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MORPHOLOGICAL VARIATION IN VICTORIAN, LOWLAND POPULATIONS OF *EUCALYPTUS PAUCIFLORA* SIEB. EX SPRENG.

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ABSTRACT: The pattern of morphological variation in isolated, lowland populations of *Eucalyptus pauciflora* was analysed phenetically using multivariate classification and ordination techniques. The main aim was to discover how variable were the lowland populations in the context: (1) of the physiological and morphological variation in the species at higher altitudes; and, (2) of the scattered nature of these sites, which are possibly relics from a wider distribution during the last glaciation. Outgroups were used as aids to interpreting the patterns.

Adult morphology showed little variation at lowland sites, although some small differences were observed, and some populations showed signs of recent hybridisation with *E. obliqua* and *E. radiata*. Within the total range of *E. pauciflora* however, seedlings showed two forms with the lower altitude populations possibly showing the ancestral condition. An equivocal large population at Wartook Reservoir, Grampians, suggested that introgression between *E. pauciflora* and *E. willisii* has occurred in the past, resulting in a stable intermediate form.

Eucalyptus pauciflora Sieb. ex Spreng. (an ash species: informal subgenus *Monocalyptus*, series *Obliquae*, Pryor and Johnson 1971) is the dominant tree at high altitudes in south-eastern Australia, occurring throughout the mountains and sub-alpine areas of eastern Victoria and New South Wales, extending marginally into Queensland and occurring throughout most of central and eastern Tasmania. The altitudinal range on the mainland is from sea level to 2000 m, but largely 730-2000 m, and in Tasmania between just above sea-level to 730 m, with limited extension up to 1,276 m (Hall, Johnston & Chippendale 1970).

Lowland populations (0-700 m) principally occur in a disjunct distribution in southern Victoria (Fig. 1). Scattered amongst these lowland populations are a few higher altitude populations at approximately 1000 m (Major Mitchell Plateau, Mt. Cole, Camels Hump). Remnant trees which occur south of Mt. Gambier in South Australia, are the most westerly occurrence of the species (Boomsma & Lewis 1981). At higher altitudes, *E. pauciflora* shows considerable morphological variation—Mueller (1879-1884) noted differences in leaf shape and fruit size in the "alpine variety"; the species later being shown to vary clinally, both morphologically and physiologically, with altitude (Pryor 1957, Green 1969, Burdon & Chilvers 1974, Slatyer 1977a, b, c, 1978, Slatyer *et al.* 1977a, b, c). This variable nature of *E. pauciflora* at higher altitudes led to the question of how variable were the isolated, lowland populations. The disjunct nature of these lowland populations has been commented on (Costermans 1981), but otherwise left unstudied. Specimens of *E. radiata* and *E. willisii* (peppermints) and *E. obliqua* (ash) were also included in this study as these taxa were suspected of being involved in hybridisation with *E. pauciflora* at some locations.

METHODS

POPULATIONS SAMPLED

In total, 20 populations of *E. pauciflora* were sampled (Fig. 1), ranging from the most westerly occur-

rence through to Wilsons Promontory. Within this range, samples of populations from isolated mountain tops, such as Mt. Cole, were also collected. Samples from Mt. Buffalo and Eildon were included as representatives of populations growing in the south-eastern alps and Tasmania respectively. Specific site localities are tabulated in Appendix 1.

In general, five trees were sampled from each locality, although the small size of some populations meant that this was not always possible. Additional samples were often taken where individuals appeared to be hybrid or morphologically variable. Trees were sampled throughout the spatial range of each population to avoid collecting closely related individuals. Fruits, buds and leaves were collected, where present, from each individual. Herbarium specimens are lodged at the University of Melbourne. Buds, and a leaf for oil gland density, were preserved in 70% alcohol; and fruits were air-dried for seed extraction and subsequent seedling growth.

SEEDLING TRIAL

Seed from 18 populations (93 parent trees) was available for the growth of seedlings. Seed was either sown directly into pots or was placed on moist filter paper in petri dishes (e.g. higher altitude populations) and stratified for 4 weeks at 4.5°C to improve germination (Hargreaves 1977). Germination in the latter occurred at a minimum one week after cold treatment. To minimise fungal growth, a small amount of Karathene was added to all petri dishes. Depending on germination rate, 1-6 seedlings were pricked into individual pots containing a general potting mixture. Each parent tree was represented by four such pots. Some seed from Powlett River (4 trees), South Australia (2 trees), Major Mitchell Plateau (1 tree) and Green Ck. Rd. (1 tree) did not germinate and appeared to be inviable. Some seed lots consisted principally of chaff and others had few viable embryos (tested by seed squash). Seedlings were grown in a heated glasshouse for 4-5 months. Pots were even-

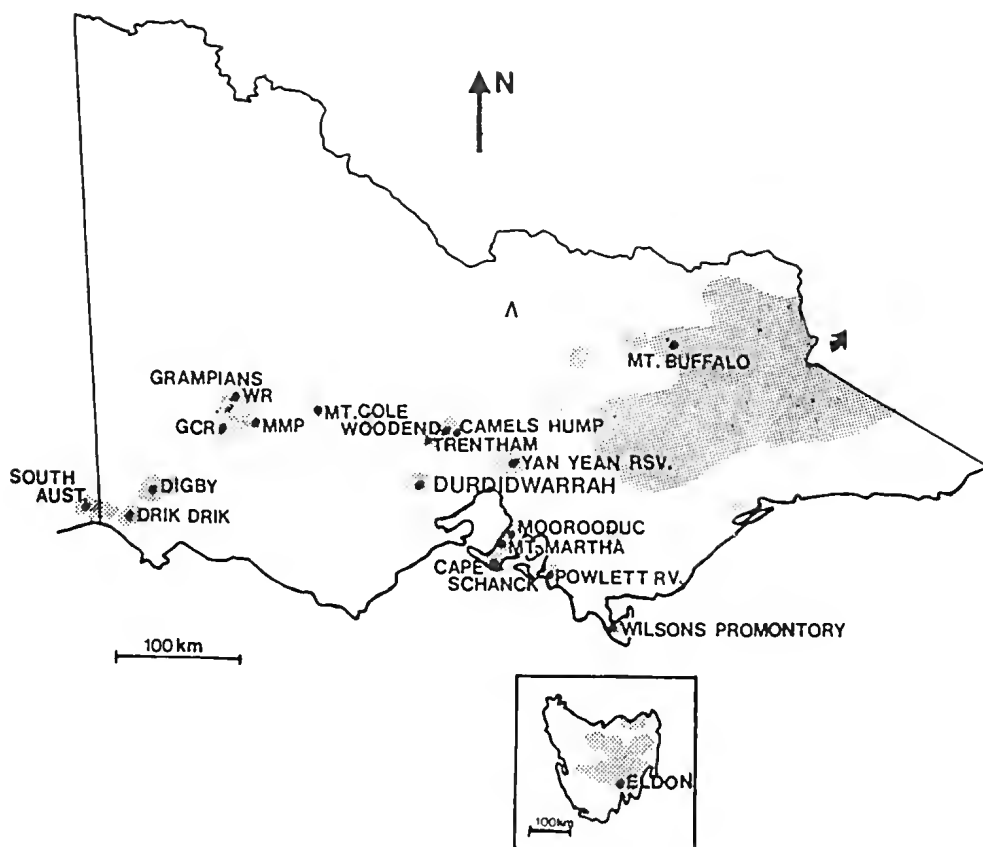


Fig. 1—Generalised distribution of *Eucalyptus pauciflora* (stippling) in Victoria, South Australia and Tasmania, with collection sites superimposed. Abbreviations: MMP=Major Mitchell Plateau, WR=Wartook Reservoir, GCR=Green Creek Road.

tually thinned to one seedling per pot, unless segregation was apparent. During the winter, four 500 W self-balasting mercury vapour lamps, photoperiod 10/14 hr, were used to supplement daylight, and seedlings were rotated to ensure maximum effectiveness.

Seedlings of *E. obliqua* (seed from Brisbane Ranges), *E. radiata* (from Eltham) and *E. willisii* (from Grampians) were grown for comparison with seedlings from alleged hybrid populations, to check for character segregation.

CHARACTERS

Adult

To cover the inherent variability within individuals, five mature leaves and ten fruits and buds were measured per tree. Twenty-six adult characters were scored (Table 1, Fig. 2). Mean oil gland density was calculated by measuring five 8 mm grids mid-lamina of each leaf. Buds were cut longitudinally to measure pedicel length since it was difficult to measure the true length externally. The form factors, measured on a digitiser, gave an indication of leaf shape, a value of 1.0 indicating a circle and 0.0 a line.

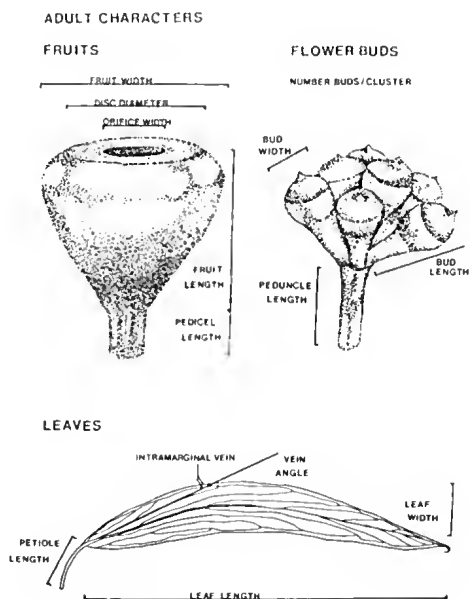


Fig. 2—Adult characters measured.

TABLE 1
ADULT CHARACTERS SCORED FOR DATA MATRICES

Binary		State
1. Leaves	dull/glossy	0/1
2. Leaf apex	with/without hook	0/1
3. Branchlets	non glaucous/glaucous	0/1
Multistates		
4. Fruit disc	Sunken/level/raised	1/2/3
Numerics		
5. Leaf length (mm)		
6. Leaf width (mm)		
7. Form factor		
8. Leaf thickness, mid lamina (mm)		
9. Secondary vein angle (°)		
10. Intramarginal vein (mm)		
11. Oil gland density, mid-lamina (per cm ²)		
12. Displacement (mm)		
13. Petiole length (mm)		
14. Maximum fruit width (W) (mm)		
15. Disc diameter (mm)		
16. Fruit length (L) (excluding pedicel) (mm)		
17. L/W ratio		
18. Diameter of orifice (O) (mm)		
19. O/W ratio		
20. Distance from widest part of fruit to disc edge		
21. Pedicel length (mm)		
22. Number of flower buds/cluster		
23. Bud length (including pedicel) (mm)		
24. Pedicel length (mm) buds cut in L.S		
25. Peduncle length, buds (mm)		
26. Maximum bud width (mm)		

$$\text{Form Factor} = \frac{4\pi p^2}{A} \text{ where } p = \text{leaf perimeter, } A = \text{area}$$

Seedlings

In total, 370 seedlings were measured for 27 characters (Table 2). The following seedling leaf stages were defined for *E. pauciflora*, counting cotyledons as node 1 (Fig. 3a). (1) Seedling leaves are opposite, in most cases petiolate, occur at nodes two to three, and only occur on seedlings. (2) Juvenile leaves are broader, opposite, petiolate, and horizontally orientated, occurring for the next one to seven nodes. They are also found as coppice. (3) Intermediate leaves show intranode formation and often a 90° twist in the petiole to orientate the leaf in the vertical plane. Leaves are broad relative to adult foliage and do not show parallel venation. Other ashes, such as *E. obliqua*, incorporated in this study, show a similar sequence of seedling stages. In comparison, the peppermints have opposite, sessile juvenile leaves for an indefinite number of nodes (Fig. 3b). The distinct differences between the two types of seedlings proved useful in the identification of hybrids.

NUMERICAL ANALYSIS

Adult trees and seedling characters were analysed using phenetic, multivariate classification and ordination techniques available in the C.S.I.R.O. TAXON package

(Ross 1982). Initially, a data matrix of all individuals (either adults or seedlings), was used to calculate a dissimilarity matrix between all pairs of individuals. Squared, standardised, Euclidean distance, was the dissimilarity measure generated by the program MSED. Both adults and seedlings were classified using an agglomerative system (SAHN) which minimised the incremental sum of squares. A dendrogram provided a two-dimensional representation of the hierarchy, and the program GCOM indicated which attributes were important in the classification. The program CRAMER also ranked attributes on their ability to discriminate between groups.

Ordination consists of displaying, in an efficiently reduced Euclidean space, the interrelationships of the entities under study (Williams, Dale & Lance 1971) and can reveal relationships which otherwise might be overlooked when a large amount of data is to be interpreted. An advantage of ordination is that entities can be shown in three-dimensional space, separating groups which may be clustered into two dimensions. In this case Principal Coordinates Analysis (PCOA) was employed. All adult individuals were ordinated but, due to the large numbers involved (370), seedlings were only ordinated

TABLE 2
SEEDLING CHARACTERS SCORED FOR DATA MATRICES

<i>Binary</i>		State
1. Stem wax	present/absent	0/1
2. Raised oil glands on stem	zero, few/many	0/1
3. Underleaf colour, node 2	purple/not	0/1
4. Leaf base, node 4	cordate/not cordate	0/1
5. Leaf base, node 5	cordate/non cordate	0/1
6. Leaf surface, node 4	dull/shiny	0/1
7. Leaf colour, node 4	green/blue-green	0/1
8. Leaf underside, node 5	discolourous/concolourous	0/1
9. Raised oil glands on leaf, node 4	absent/present	0/1
10. Lignotuber	absent/present	0/1
11. Leaf surface, node 6	green/blue-green	0/1
<i>Multistates</i>		
12. Node at which leaves alternate	nodes 3-7	1
	nodes 8-9	2
	nodes 10 and above	3
13. Node at which leaves twist	nodes 3-7	1
	nodes 8-9	2
	nodes 10 and above	3
14. Node at which leaves become petiolate	nodes 3-7	1
	nodes 8-9	2
	nodes 10 and above	3
<i>Numerics</i>		
15. Petiole length, node 2 (mm)		
16. Petiole length, node 4 (mm)		
17. Leaf length, node 4 (mm)		
18. Leaf width at widest part, node 4 (mm)		
19. Form factor, node 4 (mm)		
20. Oil gland density, node 4 (per cm ²)		
21. Secondary vein angle, node 4 (°)		
22. Intramarginal vein (mm)		
23. Petiole length, node 5 (mm)		
24. Leaf length, node 5 (mm)		
25. Leaf width at widest part, node 5 (mm)		
26. Form factor, node 5 (mm)		
27. Petiole length, node 7 (mm)		

as group centroids (average individual for each group). Gillison's (1978) technique of displaying group centroids on the third axis as a series of graded spheres was employed. BACRIV was also used to calculate the correlation of each attribute to the axes of PCOA. A minimal spanning tree (MST), used in conjunction with the ordination of group centroids, provided a network of shortest total length connecting all points under consideration such that each point is connected with every other point by a chain of links with no closed loops occurring (Gillison 1978).

RESULTS

ADULT TREES

The classification based on all adult individuals (Fig. 4) was truncated at both the ten group and five group level. The first major dichotomy separated the peppermints, *E. radiata* and *E. willisii* (Group 5), from the ashes, *E. pauciflora* and *E. obliqua* (Groups 1-4). Characters contributing to this division were vein angle,

leaf thickness and fruit size. According to GCOM, the peppermints were distinguished by a wider vein angle (20°), thinner leaves (0.22 mm) and smaller fruits (5.4 mm wide). This is in comparison with the ashes which had a vein angle of 9° (dominated by individuals of *E. pauciflora*), leaves 0.37 mm thick and fruits 8.5 mm wide on average. Of the five major groups (Fig. 4), *E. obliqua* was exclusively classified into group 4 and was characterized by a mean vein angle of 21°, oblique leaf bases and an intramarginal vein 3 mm from the leaf edge. Within *E. pauciflora*, individuals were classified into groups 1, 2 and 3: group 1 was distinguished by large fruits (9 mm wide, 9 mm long) with level discs, group 2 by uncharacteristically small fruits (6.5 mm wide, 6.5 mm long), group 3 again by large fruits (9 mm long) but with sunken discs. The division on disc position is largely artificial since the character is variable within populations, and thus some of them were split between groups 1 and 3. Cramer values for characters that best distinguish these 5 groups are shown in Table 3.

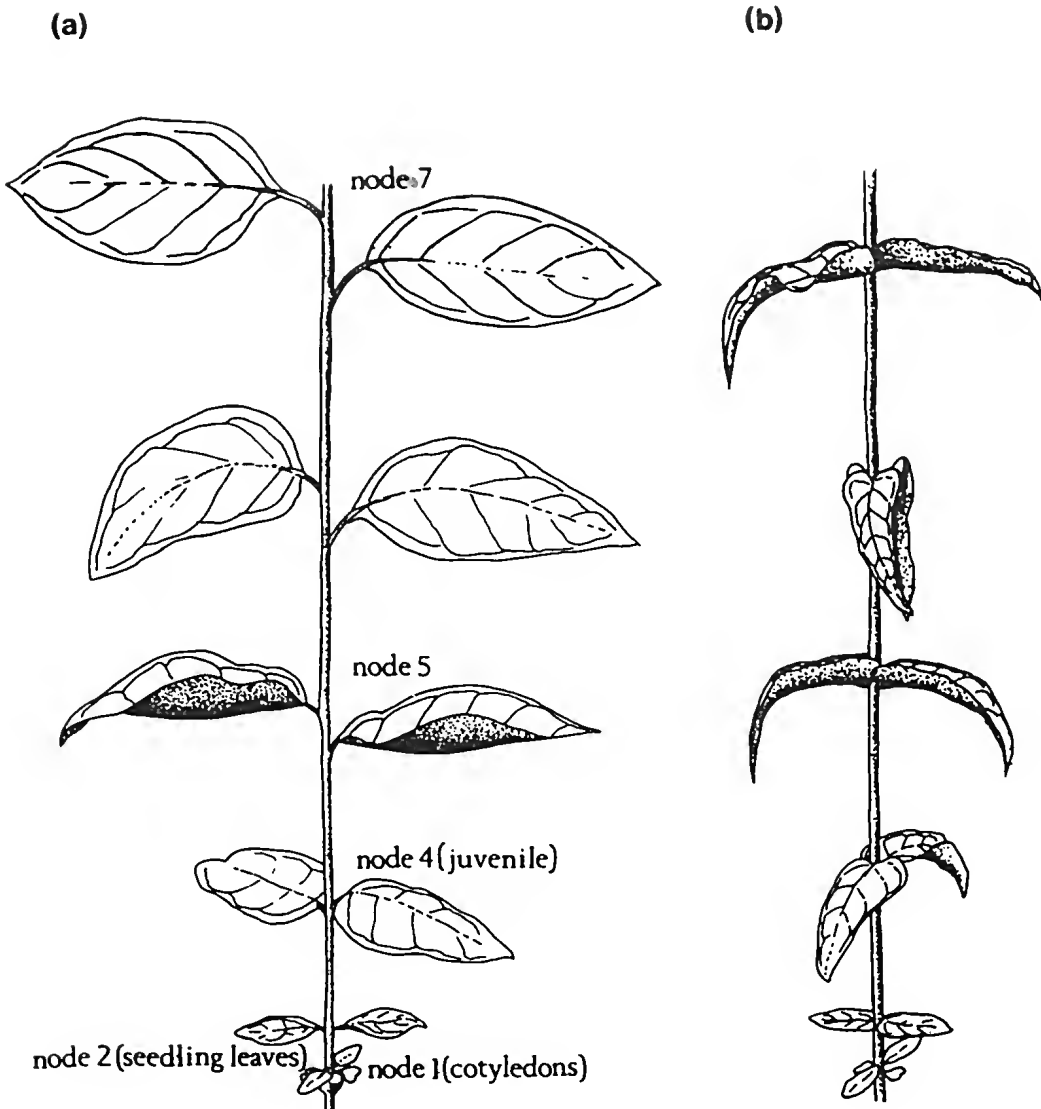


Fig. 3—(a), A typical higher altitude seedling of *E. pauciflora* showing the principal nodes measured (on all seedlings), early intranode formation and orientation in the vertical plane. (b), A typical peppermint seedling (*E. radiata*) showing sessile, opposite, juvenile leaves which occur for an indefinite number of nodes.

Fig. 4—Classification of 122 adults truncated at the five and ten group level; VA=vein angle. Percentage composition, on a population basis, of the five major groups is as follows. 1: Mooroodue 100%, Mt. Martha 80%, Durdidwarrah 100%, Trentham 60%, Woodend 100%, Camels Hump 100%, Digby 2 100%, Mt. Cole 50%, Yan Yean 100%, Green Ck. Rd. (Grampians) 40%, Mt. Buffalo 60%, Wilsons Promontory 80%, Cape Schanck 40%, Powlett River 40%. 2: Digby 1 100%, Major Mitchell Plateau 100%, Wartook Reservoir (Grampians) 100%, South Australia 50%. 3: Tasmania 80%, Powlett River 40%, Drik Drik 100%, Green Ck. Rd. 40%, Mt. Cole 50%. 4: *Eucalyptus obliqua* 100%. 5: *Eucalyptus radiata* 100%, *Eucalyptus willisii* 100%.

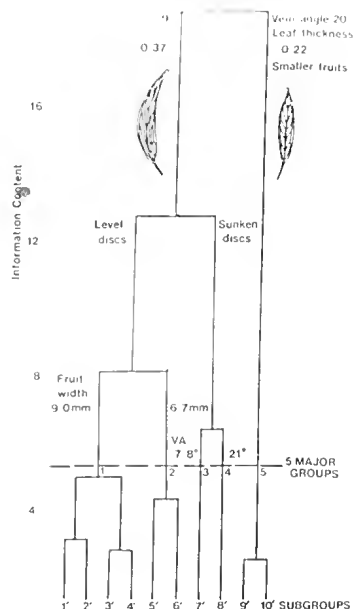


TABLE 3
CRAMER VALUES FOR CHARACTERS THAT BEST DISTINGUISH THE FIVE MAJOR GROUPS DEFINED IN THE CLASSIFICATION OF ADULT TREES. THE MEAN VALUE IS GIVEN FOR QUANTITATIVE VALUES.

Groups		Characters	
1	<i>E. pauciflora</i>	Maximum fruit width (mm)	Secondary vein angle (°)
2		9.06	8.17
3		6.68	8.52
4	<i>E. obliqua</i>	9.22	7.84
5	<i>E. radiata</i>	7.97	20.83
	<i>E. willisii</i>	5.40	20.10
		Cramer Value=0.8635	Cramer value=0.8423
		Disc diameter (mm)	Fruit length (mm)
1		7.54	8.59
2		5.72	6.42
3		7.01	9.52
4		4.98	9.15
5		4.38	4.77
		Cramer value=0.8390	Cramer value=0.8254
		Orifice diameter (mm)	Leaf thickness (mm)
1		4.30	0.39
2		3.25	0.35
3		4.26	0.35
4		3.42	0.32
5		2.41	0.22
		Cramer value=0.7811	Cramer value=0.7035

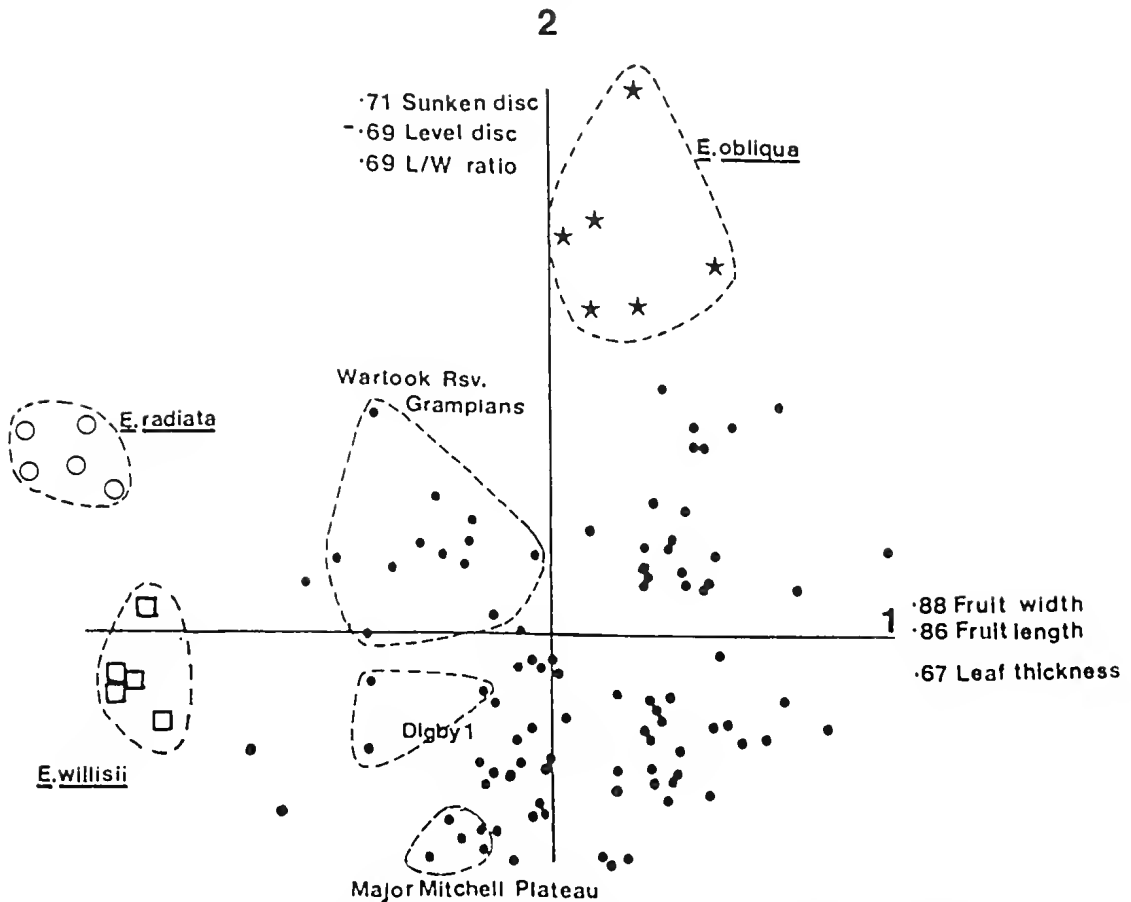


Fig. 5—Ordination of all adult individuals. Solid circles represent individuals collected as *E. pauciflora* (or putative hybrids). Character correlation coefficients are shown on axes; L/W=length/width ratio.

A comparison of the ten subgroups gives more information on the pattern of variation within *E. pauciflora*. Individual trees from any one geographic district were generally classified in the same subgroup. Five subgroups contained most of the *E. pauciflora*, and they consisted principally of the following individuals (percentage occurrence indicated): 1', Moorooduc (100%), Mt. Martha (80%) and Durdidwarrah (100%); 2', Woodend (100%), Trentham (60%), Camels Hump (100%), Digby 2 (100%) and Mt. Cole (50%); 3', Wilson's Promontory (80%) and Yan Yean (100%); 5', Digby 1 (100%), S.A. (50%) and Major Mitchell Plateau (100%); and, 7', Powlett River (40%), Tasmania (80%) and Drik Drik (100%). The trees from Powlett River and Cape Schanck were the most variable. The former were scattered through subgroups 2', 5', 6' and 7', and the latter into subgroups 3' and 7'. *E. pauciflora* in subgroups 5' and 6' were characterized by having markedly small fruit (6.9 and 6.4 mm width respectively). Subgroup 5' consisted of trees principally from Major Mitchell Plateau and Digby 1; while 6' almost exclusively consisted of individuals from Wartook Reservoir, Gramplains. It is interesting to note that, although fruit size of individuals from 5' and 6' are in-

termediate, their leaves are 0.35 mm thick, similar to those of *E. pauciflora* (0.35-0.43 mm) and different from peppermints which had relatively thin leaves (0.18-0.25 mm). Three trees from Mt. Buffalo were the only individuals in subgroup 4', having broader, shorter leaves than the others (form factor 0.43). Subgroups 1', 2', 3' and 7' show similar measures over most leaf and fruit characters, although individuals in 2' were characterized by glaucous stems and individuals in 7' had sunken discs similar to *E. obliqua*.

Two ordinations are included, one ordinating individual trees and one the ten groups from the classification. The ordination of all individuals (Fig. 5) accounted for 41% of the total information in the first two axes and 51% on the first three. Individual trees of *E. radiata*, *E. willisii* and *E. obliqua* form recognizable clusters equivalent to the groups in the classification. These represent outgroups for interpreting the pattern within *E. pauciflora*. Fruit size was the most important character separating individuals on axis 1. Populations from Wartook Reservoir, Digby 1 and Major Mitchell Plateau are intermediate between the peppermints *E. radiata* and *E. willisii*, and the most distinctive largest fruited form of *E. pauciflora*. Individuals on axis two

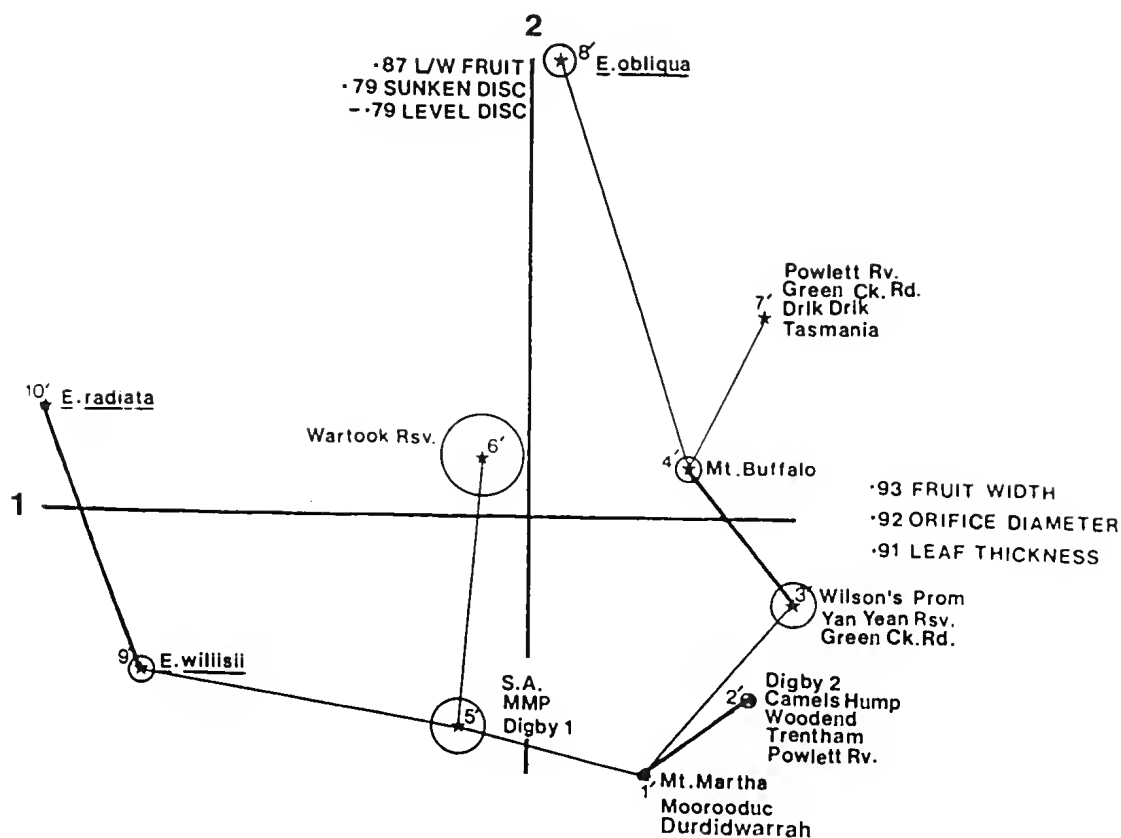


Fig. 6—Ordination of the group centroids of subgroups 1'-10' defined by the classification of all adult individuals; MMP=Major Mitchell Plateau, S.A.=South Australia, L/W=length/width ratio. Links join nearest neighbours. Axis 3 is represented as the diameter of the spheres. Darker lines indicate a reciprocal link. Character correlation coefficients are shown on axes.

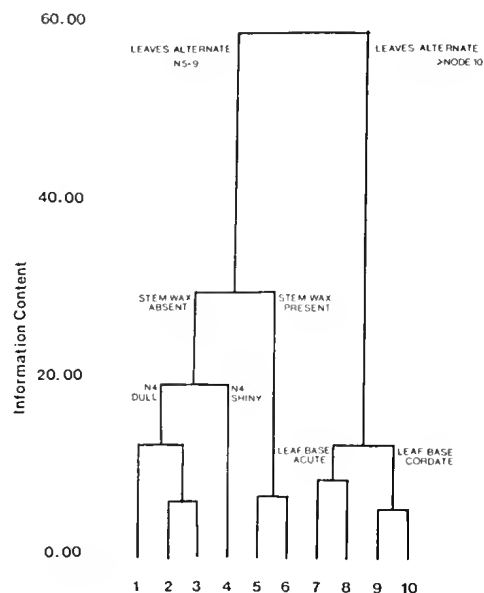


Fig. 7—Classification of seedlings of *E. pauciflora* (with some *E. obliqua* and *E. radiata*) truncated at the ten group level; N=node. General percentage composition of groups 1-10 is as follows. 1: Moorooduc 90%, Cape Sehanek 50%, Mt. Martha 80%, Durdidwarrah 90%, Trentham 40%, South Australia 56%. 2: Digby 2 50%, Green Ck. Rd. 50%, Woodend 30%. 3: Powlett River 45%, Green Ck. Rd. 38%. 4: Cape Sehanek 20%, *E. obliqua* 100%. 5: Woodend 50%, Mt. Buffalo 40%, Tasmania 40%, Camels Hump 40%, Trentham 20%. 6: Mt. Cole 86%, Major Mitchell Plateau 90%, Tasmania 60%, Mt. Buffalo 60%, Camels Hump 50%. 7: Wartook Reservoir 67%, *E. willisii* 78%. 8: *E. willisii* 22%, Wartook Reservoir 23%. 9: Powlett River 26%, Digby 1 75%. 10: *E. radiata* 90%, Powlett River 19%.

TABLE 4

CRAMER VALUES FOR CHARACTERS THAT BEST DISTINGUISH THE TEN MAJOR GROUPS DEFINED IN THE CLASSIFICATION OF THE SEEDLINGS. FOR QUALITATIVE CHARACTERS THE PERCENTAGE FREQUENCY OF SEEDLINGS IN EACH STATE IS GIVEN; FOR QUANTITATIVE CHARACTERS THE MEAN VALUE FOR THE CHARACTER IS GIVEN.

Groups		Characters			
	State	Node 4, dull/shiny		+ stem wax	
		0	1	0	1
1		100%	0	100%	0
2		100	0	97.4	2.6
3		100	0	100	0
4		0	100	100	0
5		100	0	9.4	90.6
6		96.3	3.7	11.3	88.7
7		100	0	98.0	2.0
8		100	0	100	0
9		100	0	96.8	3.2
10		100	0	100	0
		Cramer value = 0.9388		Cramer value = 0.9075	
	State	+ lignotuber		Node 7, petiole length (mm)	
		0	1		
1		0	100%		4.95
2		5.3	94.7		7.38
3		0	100		3.76
4		0	100		9.96
5		28	72		8.74
6		0	100		13.14
7		0	100		1.62
8		100	0		1.26
9		0	100		0.56
10		0	100		0.13
		Cramer value = 0.8495		Cramer value = 0.8488	
		Node 5, petiole length (mm)		Node 5, leaf width (mm)	
1		2.23		47.14	
2		2.81		56.92	
3		0.88		53.14	
4		3.97		43.27	
5		3.14		49.25	
6		5.64		58.47	
7		0.34		33.20	
8		0.68		36.05	
9		0.08		39.23	
10		0.00		31.12	
		Cramer value = 0.7918		Cramer value = 0.7218	
		Node 5, form factor		Node 4, leaf width (mm)	
1		0.82		35.62	
2		0.75		48.08	
3		0.80		41.14	
4		0.65		38.38	
5		0.79		40.87	
6		0.79		49.36	
7		0.59		33.22	
8		0.65		32.41	
9		0.75		34.33	
10		0.62		27.44	
		Cramer value = 0.7126		Cramer value = 0.7080	

TABLE 4 continued

Groups	Characters			
	Node 4, petiole length (mm)		Node/leaves alternate	
	State	1(3-7)	2(8-9)	3(10-)
1	2.20	13.7%	74	12.3
2	1.83	68.4	29	2.6
3	0.79	29.7	56.7	13.6
4	2.40	93.3	6.7	0
5	2.45	62.5	37.5	0
6	3.27	75.5	24.5	0
7	0.33	0	4.0	96.0
8	0.77	4.5	13.6	91.9
9	0.50	0	16.1	83.9
10	0.00	0	5.5	94.5
	Cramer value = 0.7037		Cramer value = 0.6981	

separate on whether they have a level or sunken disc. As populations of *E. pauciflora* show variation in disc position they are separated on this axis. The ordination of the ten subgroups includes a minimum spanning tree linking nearest neighbours (Fig. 6). The first three axes account for 75% of the total variation. Fruit, leaf and bud characters are correlated with axis one. The interesting point of this ordination is the link between individuals from Wartook Reservoir and other small-fruited individuals in subgroup 5'. The intermediate position of the subgroups 5' and 6', and hence individuals from Wartook Reservoir, Major Mitchell Plateau and Digby 1, is also quite clear on the ordination. A reciprocal link between subgroups 1' (Moorooduc, Mt. Martha and Durdidwarrah) and 2' (Camels Hump, Woodend and Trentham), indicates similar morphology in these populations (fruits 8-9 mm long, 9 mm wide, leaves 0.37 mm thick). Trees within each of these groups are broadly speaking from the same geographic regions, and so may be subject to similar climatic and edaphic conditions.

SEEDLINGS

The classification of all seedlings (Fig. 7) was truncated at the ten group level. The major dichotomy was based on the node at which leaves alternate. Groups 1-6 consist of ash-like seedlings (alternation nodes 5-10), and groups 7-10 of peppermint-like seedlings (alternation nodes 8-indefinite). Within the ashes, all seedlings from localities of 1,000 m altitude and above, from Tasmania, and a few from Woodend occur in groups 5 and 6. As GCOM and CRAMER indicate (Table 4), these populations are characterized by all seedlings being glaucous. Groups 1-3 consist virtually of all lowland populations of *E. pauciflora* (percentage frequency of population composition for these three groups is shown in the caption to Fig. 7).

Three ordinations of the seedling data were subsequently run. The ordination of the ten groups generated by the classification showed many characters highly positively correlated with axis one, although groups were principally separated on petiole length and the

node at which intranode formation occurs (Fig. 8). An important point illustrated in this ordination is the presence of seedlings from Powlett River in groups 3 (*E. pauciflora*), 9 (Digby 1—intermediate) and 10 (*E. radiata*). Seedlings from individuals were split between these three groups, indicating character segregation, and hence hybridisation at this locality. Cape Schanck seedlings occurred in groups 3 and 4 (the latter including *E. obliqua*), again strongly indicating recent hybridisation. Wartook Reservoir seedlings which had questionable parentage were very similar to peppermint seedlings in having opposite, blue-green leaves for many nodes. They showed, however, distinct ash characters of petiole formation and a change in leaf orientation around nodes 7-8 (Fig. 9). There was, however, no sign of segregation, suggesting recent hybridisation is less likely. The position of groups 5 and 6 (higher altitude) on the plot indicate they generally have longer petioles and alternate at an earlier node than the lower altitude seedlings. The ordination of seedlings from the fourteen populations (Fig. 10), excluding those showing recent hybridisation, further highlighted the separation between lower and higher altitude sites. The program NEAREST indicated a very weak link between groups 4 (Trentham) and 14 (Camels Hump), as shown by the dashed line. This program separates all populations from above approximately 1,000 m and Tasmania from all lowland populations. Again, high altitude seedlings show longer petioles (10-15 mm at node 7) and earlier alternation (generally nodes 5-7) than the lower altitude seedlings which show petioles 2-8 mm in length at node 7 and alternation ranging from nodes 5-10 (most showing later alternation around nodes 8-10; see Fig. 11). Of the total variation in the ordination of Fig. 10, 72% was retained in the first three axes. One of the most important characters separating populations is the presence of wax, all high altitude individuals, apart from a few from Major Mitchell Plateau, being glaucous. Regional variation seen in the adults is reflected in the seedlings, with some clustering around the Mornington Peninsula/Durdidwarrah and Woodend/Camels Hump districts. Looking at characters over all populations, petiole length at node 7

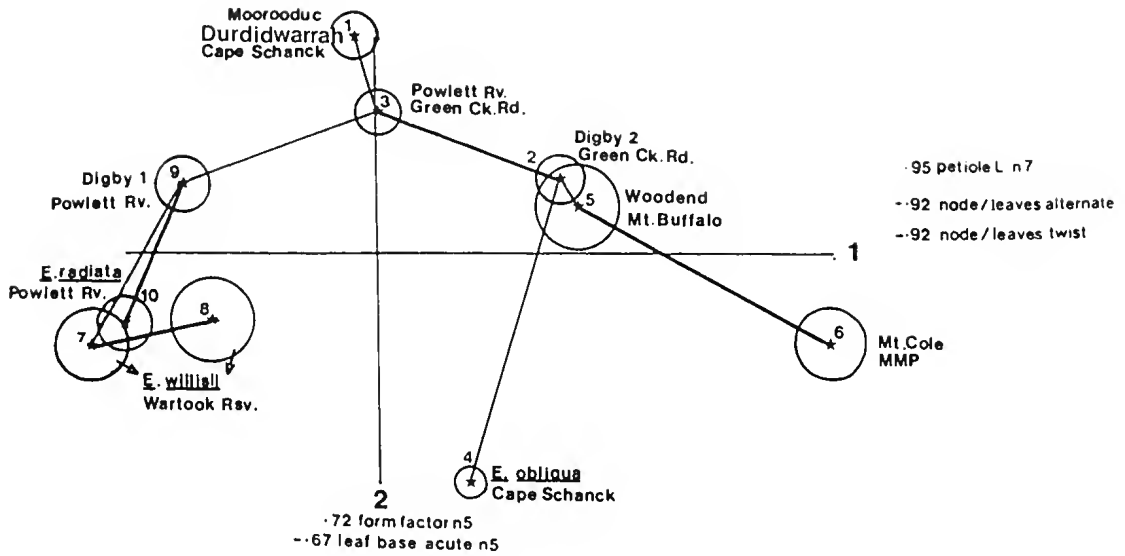


Fig. 8—Ordination of group centroids of the ten groups defined in the classification of all seedlings. Links join nearest neighbours; axis 3 is represented as the diameter of the spheres; with character correlation shown on axes 1 and 2. For complete group composition see caption of Fig. 7; MMP = Major Mitchell Plateau, L = length, N = node.

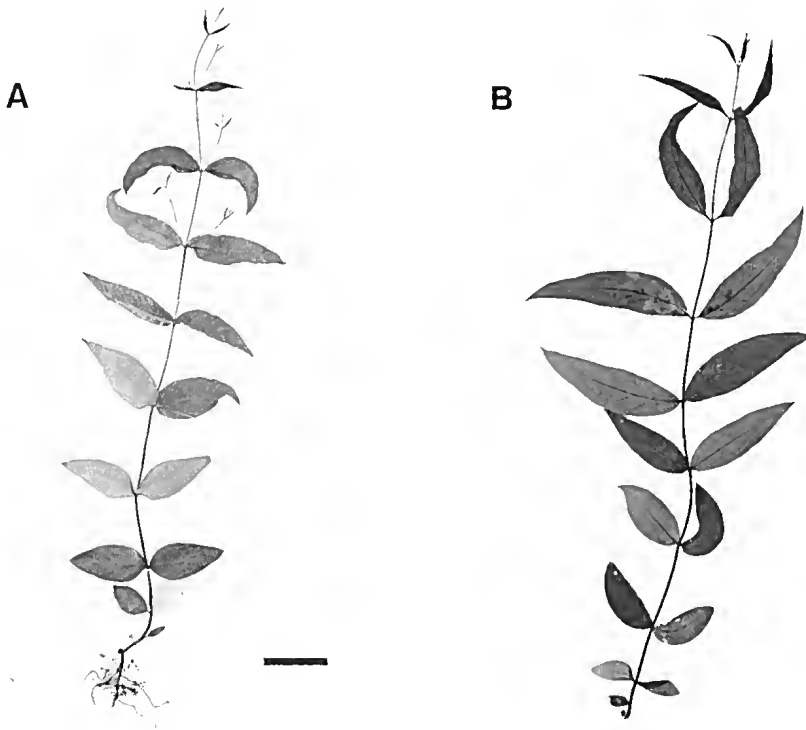


Fig. 9—Seedlings from individuals of: (A) *E. willisii*, Mirranatwa Gap, Grampians and (B) the equivocal population at Wartook Reservoir, Grampians. Scale: 5 cm.

varied quite markedly, ranging from 2 mm in South Australia to 15 mm at Mt. Buffalo. Apart from the South Australian population, western district populations separate on axis two, most possessing raised oil glands on the margin of node 4. The significance of this character is uncertain. The displacement of the South Australian population on axis three, on which oil gland density is negatively correlated (Table 5), is due, in part, to a low oil gland density (23 cm⁻²).

Populations from the Grampian Ranges warranted special attention, consequently all individuals from that region were ordinated separately, with 49% of the total variation being accounted for in the first three axes (Fig. 12). Seedlings of *E. pauciflora* collected at two localities are relatively distinct, again showing a trend to longer petioles and earlier intranode formation at higher altitudes, as shown by the correlation coefficients (Fig. 12). There is, however, some overlap, indicating a morphological gradient between the two forms. Open circles in Fig. 12 indicate seedlings from individuals thought to be *E. willisii*, collected at Mirranatwa Gap; the seedlings from Wartook Reservoir (closed circles) are quite peppermint-like, emphasised by the overlap of the open and closed circles. Compared to the spread in seedlings of *E. pauciflora* on this plot, the Wartook Reservoir individuals show consistent characters. Leaf length is positively correlated with axis three (Table 8), the seedlings of *E. pauciflora* generally having longer leaves (113-125 mm, node 5) than the Wartook Reservoir individuals (95.7 mm, node 5).

DISCUSSION

REGIONAL PATTERNS

Lowland populations of *E. pauciflora* were relatively

similar overall, most being of woodland form and gum-barked to the base, although trees at Trentham were of forest form and some others had a rough-barked butt. Fruits ranged between 8-11 mm wide and disc position varied within populations from level to sunken. Leaf length varied (114 mm at Camels Hump to 175 mm at Digby), but overall leaves were narrow (average of 25 mm), slightly falcate, acuminate with a hook, and showing distinctive parallel venation. Buds (7-15 per axillary cluster) remained relatively consistent in shape throughout the range). All populations from higher altitudes (e.g. Camels Hump), had glaucous fruits and stems as well as some trees from Digby (120-160 m a.s.l.). The relative similarity of individuals over all populations at lower altitudes suggests a general uniformity of habitat and therefore, lack of intense selection pressures at lower altitudes. At higher altitudes populations of *E. pauciflora* show variation in a number of physiological and morphological characters with changing elevation. Thus the species seems to have the capacity to adapt in response to different habitats. Pryor (1957) suggested that when looking at the association between growth rate and altitude of origin, other factors beside elevation come into effect at lower altitudes. This is probably also the case with other morphological and physiological parameters.

The similarity of some populations of *E. pauciflora*, identified as regional forms, may be due to similar environmental conditions. Durdidwarrah and Moorooduc populations both occur on Tertiary acid, sandy-clay sediments (Douglas & Ferguson 1976) providing similar growth substrates. These populations have fruits about 8 mm long, thick leaves and are non-glaucous. It is this last character that appears to differentiate the Mornington Peninsula populations from those in the Wood-

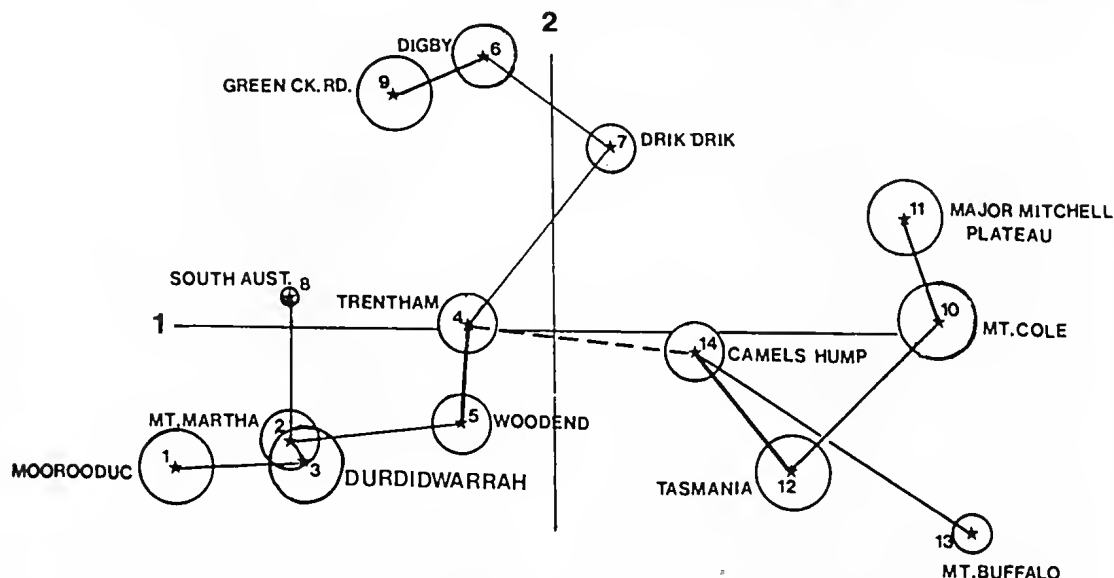


Fig. 10—Ordination of the fourteen seedling populations. Links join nearest neighbours. The dashed line indicates a weak link. Axis 3 is represented as the diameter of the spheres.



Fig. 11 — Seedlings of *E. pauciflora* grown from individuals collected at: (A) Digby, (B) Mt. Martha, (C) Major Mitchell Plateau, (D) Mt. Buffalo, illustrating the differences in intranode formation and petiole length at the different altitudes. Scale: 5 cm.

TABLE 5
THE MOST IMPORTANT CHARACTERS (FROM BACRIV) THAT CORRELATE WITH AXES ONE, TWO AND THREE
OF THE ORDINATION OF THE FOURTEEN SEEDLING POPULATIONS OF *E. pauciflora*

	Character	Correlation coefficient
Vector 1	Node 7, petiole length (mm)	0.9384
	Node 5, petiole length (mm)	0.9240
	Node 4, blue green	0.8872
	Node/leaves twist	-0.8095
	Stem wax present	0.8047
Vector 2	Node 4, raised oil glands on leaf margin	0.8009
	Node 4, leaf length (mm)	0.7182
	Node 6, blue green	-0.7087
Vector 3	Oil gland density (cm ²)	-0.5636

end district. Apart from the glaucous character, populations from the two areas show similar adult morphology, indicating perhaps a widespread regional form. The reflection of this regional variation in the seedlings suggests, in part, a genetic basis for the pattern. Pryor (1976) noted the diagnostic importance of juvenile leaves, stating that they were useful markers in genetic analysis. Consequently the variation in seedling characters is an important factor when looking at the overall pattern. The differentiation between low and higher altitude seedlings was seen in each analysis. With minor exceptions, seedlings from populations from 1,000 m or above, or those from Tasmania with a colder climate, were glaucous and generally showed a more rapid transition to intermediate foliage (nodes 5-7) and longer petioles (10-14.6 mm) than did lower altitude seedlings (nodes 6-10, 3.8-8.0 mm) (Fig. 11). Other minor variations included leaf shape, such as some seedlings from Moorooduc having more orbicular leaves than those from higher altitudes. Trees from Major Mitchell Plateau (Grampians) produced typical higher altitude seedlings of *E. pauciflora*, with long petioles, rapid transition to intermediate foliage and glaucousness. Considering seedlings are such useful genetic markers, it appears that the small fruits of trees from the Major Mitchell Plateau are due to variation within *E. pauciflora* rather than hybridisation with *E. willisii*, as there appears to be no other peppermint characters evident.

Using information from a cladistic analysis of *Monoclyptus* (Ladiges, Humphries & Brooker 1983), outgroup comparison suggests that earlier transition to intermediate foliage is a derived (advanced) character. Thus lower altitude seedlings are perhaps showing the ancestral condition. This is interesting in relation to previous suggestions of a single gene pool (Slatyer & Morrow 1977), and a widespread lowland population of *E. pauciflora* during the last glaciation (Dodson 1975). It is not possible, of course, to say unequivocally what the evolutionary history has been, but one alternative is that, with the advent of the warmer Holocene, some of the lowland populations of *E. pauciflora* migrated and adapted to higher altitudes. The present-day,

isolated, lowland populations are possibly relics, their demise being due, in part, to competition from other, more vigorous, eucalypts adapted to the warmer conditions.

RECENT HYBRIDISATION

Variable adult characters in individuals from Powlett River and Cape Schanck suggested recent hybridisation. Seedling segregation strongly indicated hybridisation was occurring between *E. pauciflora* and *E. obliqua* at Cape Schanck, and between *E. pauciflora* and *E. radiata* at Powlett River. Trees of the putative parental species were present at each site.

INTROGRESSION?

The equivocal population from Wartook Reservoir, Grampians, is not as readily explained as other morphologically different populations. Adults had small, peppermint-like fruits 6-7 mm long yet leaves showed parallel venation, a distinct Snow Gum character. Leaf thickness approached that of *E. pauciflora* in comparison to the relatively thin peppermint leaves. Bark was variable, ranging from totally gum-barked to decorticated bark on the primary branches. Data from the seedling trial proved even more interesting. Juvenile leaves were narrow, blue-green, and opposite for many nodes and in this respect were very similar to seedlings grown from the peppermint, *E. willisii* (from individuals collected elsewhere in the Grampians). The Wartook Reservoir seedlings, however, became petiolate around node 8, sometimes earlier, and showed orientation in the vertical plane, also around node 8 (both ash characters). Furthermore, seedling characters were relatively consistent, with no suggestion of segregation. The possession of some distinctive ash-like characters in what overall appears to be a peppermint, raises the question of whether introgressive hybridisation has played a part in the evolution of the Wartook Reservoir population. The extent of the gene transfer in Grampians populations, the geographic range and the pattern of variation of this form need close study before the evolutionary and taxonomic implications can be resolved. It is noted in passing that *E. vitrea* R. T. Baker, described from a

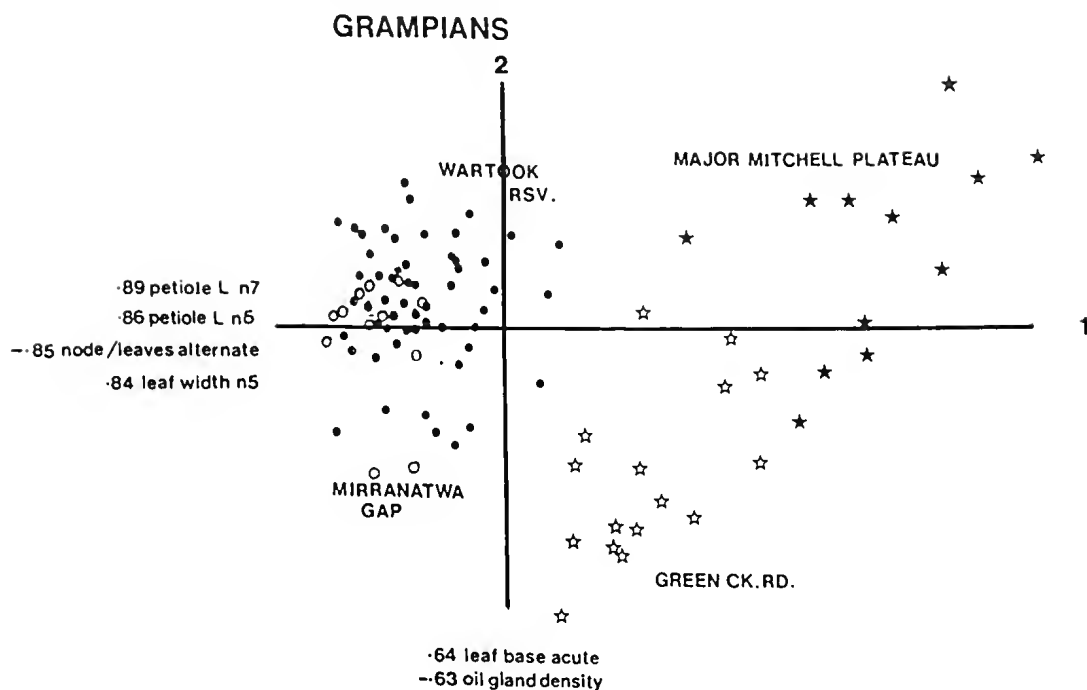


Fig. 12—Ordination of all seedlings from populations in the Grampians; character correlation coefficients are shown on axis 1 and 2; L = length, N = node. Stars indicate *E. pauciflora* seedlings, open circles seedlings from *E. willisii* at Mirranatwa Gap, and closed circles, the equivocal form collected at Wartook Reservoir.

population in Crookwell, N.S.W. (Baker 1900), has been applied to some populations in the Grampians (Sibley 1967, Parsons, Scarlett & Rosengren 1972). However, the type specimen has been described as a putative hybrid between *E. pauciflora* and *E. radiata* (Pryor & Johnson 1971). If specific rank were appropriate for the Wartook Reservoir population, then the epithet *vitrea* should probably not be used.

CONCLUSION

Overall similarity in adult morphology of lowland populations suggests less intense selection pressures are acting at lower elevations. Evolutionary implications are discussed, taking into consideration the scattered nature of the populations (possibly relics) and the differences in seedling morphology between 'low' and 'high' altitude forms. *E. pauciflora* probably was quite widespread at lower altitudes during the last glaciation. At some stage *E. pauciflora* may have been involved in the evolution, by introgression with *E. willisii*, of a stable form at Wartook Reservoir (Grampians), but extensive sampling is required for corroboration.

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APPENDIX 1
LOCALITIES OF POPULATIONS OF *E. pauciflora*; INCLUDING INDIVIDUAL TREE NUMBERS.

Site	Rainfall mm	Soil/geology	Altitude M	Associated eucalypts
1-5 Moorooduc, Frankston-Flinders Rd., Calder's (1972) site No. 34.	762	Yellow podzol/ Tertiary sandstone	46	<i>E. ovata</i>
6-10 Cape Sehanck, Calder's (1972) site No. 186.	762	Yellow podzol	76	<i>E. obliqua</i>
11-15 Mt. Martha, Forest Dvc., Calder's (1972) site No. 65.	762	Yellow podzol/ granite	152	<i>E. ovata</i> <i>E. viminalis</i>
16-20 Durdidwarrah, on road to Mercedith.	550	Laterite capping/ Tertiary sediments	380	—
21-25 Trentham, 2.2 km west to Tylden, Trentham Rd.	762-1016	Basalt	640	<i>E. viminalis</i>
26-30 Woodend, 4.5 km east of Carlsruhe, on Newham Rd.	762	Sandstone/ mudstone	540	<i>E. rubida</i>
31-40 Powlett River, "Manuka Ridge" property of Clive Hollins.	762-1016	Old sand-dune system/coffee roek	0-20	<i>E. viminalis</i> <i>E. ovata</i> , <i>E. radiata</i>
41-43 Digby 1, 1.5 km along the Digby- Strathdownie Rd.	762-1016	Sandstone	140-160	<i>E. ovata</i> (1 & 2) <i>E. baxteri</i> (1)
44-47 Digby 2, 4 km along the Digby- Strathdownie Rd.	762-1016	Sandstone	140-160	<i>E. ovata</i> (1 & 2) <i>E. baxteri</i> (1)
48-50 Drik Drik, 4.8 km S.E. of Drik Drik.	762-1016	Inland dunes	140-160	<i>E. ovata</i>
51-54 South Australia Caroline State Forest, south of "Broomfield" off Caroline Rd.	762-1016	Inland dunes	140-160	<i>E. baxteri</i> <i>E. viminalis</i>
55-64 Wartook Reser- voir Grampians. Bounded by Smith Rd. and Roses Creek Rd.	760-780	Sandstone	440-480	<i>E. viminalis</i> <i>E. baxteri</i> <i>E. obliqua</i>
65-69 Green Ck. Rd. 3.8 km N., junction of Victoria Valley Rd. and Green Ck. Rd., Grampians.	510	Granite	260	<i>E. aromaphloia</i> <i>E. obliqua</i>
70-73 Mt. Cole, Western Victoria.	762	Granite	914	—
74-78 Major Mitchell Plateau.	760-780	Sandstone	1017	<i>E. alpina</i>
79-83 Tasmania, Eildon near Hungry Flats.	762	Triassic stratified roek	470	—
84-88 Mt. Buffalo National Park, near carpark and chalet.	> 1500	Granite	1470	—
89-92 Camels Hump, near Mt. Macedon.	762	Volcanic	1011	—

APPENDIX 1 *continued*

Site	Rainfall mm	Soil/geology	Altitude M	Associated eucalypts
93-97 Wilsons Promontory north of the National Park, near Vereker Ranges.	760-780	Old sand-dunes	10-20	<i>E. viminalis</i> <i>E. obliqua</i>
98-102 Yan Yean Reservoir catchment area, track 3.	762-1016	Alluvium	200	<i>E. ovata</i>

* Rainfall data taken from Watt (1937).

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PREDATION PATTERNS AMONG MOLLUSCS IN THE
VICTORIAN TERTIARY

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ABSTRACT: The distinctive boreholes produced by two members of the predatory gastropod families, Muricidae and Naticidae, can be recognised in their molluscan prey in a fossil assemblage from the Victorian Tertiary (Pliocene) from Muddy Creek near Hamilton. Naticids are found to prey mainly on pelecypods with particular concentration on a few genera. Preferential siting of boreholes is established for two species and the degree of shell ornamentation is found to be a deterrent to successful drilling. Muricids are rare but along with naticids show a strong preference for the juveniles of one species of pelecypod.

A review of the literature concerning predation patterns amongst fossil molluscs indicates that the topic has received considerable attention. Almost certainly, this is due to the fact that it is one of the few areas where a mathematical approach can be applied to palaeopredation (Reyment 1971). Predatory gastropods that attack by drilling holes into the shells of their prey can be divided into two groups. The family Naticidae (order: Mesogastropoda) and the family Muricidae (order: Neogastropoda) are the main predatory gastropods and they show distinct differences in borehole morphology allowing each hole to be classified as to the family of the predator. The method by which the holes are drilled with the radula by these gastropods has been studied by a number of workers (Jensen 1951, Carricker 1961, Carricker and Yochelson 1968, Vermeij 1980) and the result is strong confirmation for an unequivocal determination of the type of gastropod based on the bore shape. Naticids drill a parabolic hole with a countersunk margin whereas muricids drill a more cylindrical steep-sided bore with no countersinking. A schematic diagram of both types of drill is shown in Fig. 1.

The site from which the fossils were collected is Macdonald Bank on the Muddy Creek, 6 km west of Hamilton, Victoria. A section of the bank was cleaned of weathered surface and a cubic sample (volume 27 dm³) was collected and analysed. The age of the assemblage is Lower Pliocene (Douglas and Ferguson, 1976) and it is usually referred to as the Grange Burn Coquina. Identification of the species present in the sample was carried out by Dr. T. A. Darragh of the Museum of Victoria.

RESULTS AND DISCUSSION

The species collected and number of specimens drilled or partially drilled are shown in Tables 1 and 2. Table 3 shows the species ranked in order of predation intensities. Only those species with ten or more individuals in the sample were placed in the ranked table. *Placamen subroboratum*, *Glycymeris halli* and *Sunetta gibberula* are the preferred species for naticids amongst the pelecypods, whilst muricids select *Notocorbula ephamilla*. Amongst the gastropods, naticids and muricids both prefer *Niotha crassigranosa* with other species showing little predation. There is some evidence

of cannibalism with *Polinices cunninghamiensis*—the dominant predatory gastropod sampled—showing a 1% attack rate. Reporting on cannibalism amongst gastropods from Ameke, Nigeria, Adegoke and Tevesz (1974) found naticid/naticid predation levels of 15%. Carricker (1961) reported cannibalism in laboratory starved specimens of naticids; and noted that when bivalve prey was presented, the naticids abandoned cannibalism. The greatest proportion (>99%) of naticids are *Polinices cunninghamiensis* and presumably this species is responsible for most of the naticid boreholes observed.

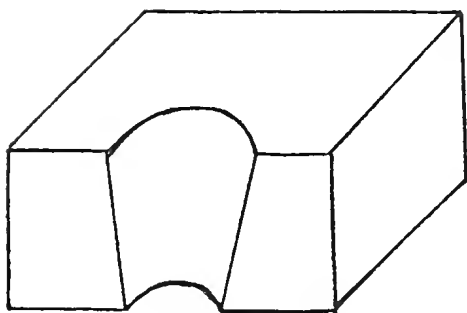
Although no muricids were found in the study sample, they have been recorded from the Muddy Creek locality. In a catalogue of Tertiary Mollusca from Australia, Darragh (1970) lists ten muricid genera, including two species of *Bedevela*, whose type locality is the Muddy Creek deposits.

Naticids accounted for between 70% and 75% of all successful drills in gastropods and pelecypods whilst muricids accounted for 25% of gastropod and 15% pelecypod drillings.

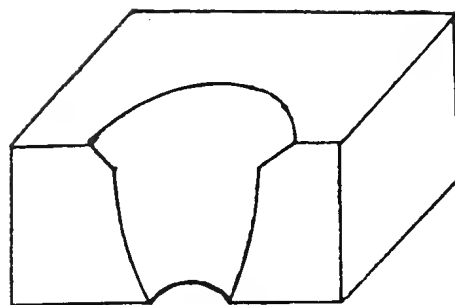
The number of left and right valves was counted for *Sunetta gibberula*, *Notocorbula ephamilla* and *Ennucula kalinniae*, and the total number of left hand valves was not significantly different from the total number of right hand valves. For individual species, there appears to have been some *post mortem* sorting; but overall the assemblage, as represented by these three species, would seem to have come from shallow water close to the shoreline.

Distribution of drilled holes in pelecypod shells

The two species chosen for this investigation were *Sunetta gibberula* and *Glycymeris halli*. This choice was made in view of the need to have adequate sample numbers for the statistical analysis. The data for the analysis were obtained by projecting an image of the valve onto a screen using an overhead projector. The projector was moved until the shadow of the valve coincided with the outline traced from a typical valve of median size. By using this method, the position of the borehole showed as a spot of light and it was possible to obtain relative positions of boreholes regardless of the size of the valve. Figure 2 shows the scatter diagram for



Muricid borehole



Naticid borehole

Fig. 1—Typical predation boreholes by muricids (left) and naticids (right).

TABLE 1
OCCURRENCE OF DRILLHOLES IN GASTROPODS FROM THE GRANGE
BURN COQUINA

Species	Total Examined	Drilled Naticid	Drilled Muricid	Failed Drills
<i>Allocochira papillata</i> (Tate)	50	1		1
<i>Austromitra</i> sp.	1	1		
<i>Gemmaterebra catenifera</i> (Tate)	25	2		
<i>Polinices cunning-</i> <i>hamensis</i> (Harris)	205	3		
<i>Semicassis wannonensis</i> (Tate)	1	1		
<i>Sydaphera wannonensis</i> (Tate)	8	1		
<i>Niotha crassigranosa</i> (Tate)	72	5	5	

No evidence of drilling was found in *Anaea triplicata* (Tate), *Amblychilepas* sp., *Amorena masoni* (Tate), *Ancilla* sp., *Cominella* sp., *Cymatiella verrucosa* (Reeve), *Euriclanculus eucarinatus* (Ludbrook), *Leiopyrga quadricingulata* (Tate), *Marginella* sp., *Polinices subinfundibulum* (Tate), *Polinices subvarians* (Tate).

G. halli with the arbitrary quadrats chosen for the analysis. The method of statistically treating the data obtained follows that of Reymont (1971, p. 140) in that the data were compared with a theoretical Poisson distribution and tested for goodness of fit with a chi squared test. The calculations are set out in the Appendices. The chi squared calculation was performed on the pooled data of several cells to avoid the problem of any expected cell frequency being less than 5. Kreyszig (1970, p. 249) mentioned that failure to pool classes in such cases may give unreliable results. The results of the analysis showed that the observed distribution differed significantly ($p < 0.05$) from a Poisson distribution and

that the siting of attack is not random for naticid predation of *G. halli*. The preferred area is readily seen on the scatter diagram and lies in the median section of the valve commencing at a quarter of a diameter from the umbo and extending to three-quarters of a diameter from the umbo. No preference for either side of the valve was found, with 27 borings to the left side of the arbitrary bisector and 29 borings to the right. This could be expected in a pelecypod like *G. halli* which has a perfectly symmetrical shell and there would be no orientation clues to enable a predator to drill either side selectively. In view of the symmetrical nature of the shell and

TABLE 2
OCCURRENCE OF DRILLHOLES IN PELECYPODS FROM THE GRANGE
BURN COQUINA

Species	Total Examined	Drilled Naticid	Drilled Muricid	Failed Drills
<i>Ennucula kalimnae</i> (Singleton)	158	9		1
<i>Gari hamiltonensis</i> (Tate)	9	2		
<i>Glycymeris</i> sp.	16	1		
<i>Glycymeris halli</i> (Prichard)	309	56	10	2
<i>Limopsis beaumaris-</i> <i>ensis</i> (Chapman)	26	1		
<i>Notocorbula ephamilla</i> (Tate)	184	15	8	5
<i>Ostrea</i> sp.	4	Indeterminate drills		
<i>Placamen subroboratum</i> (Tate)	103	15	2	9
<i>Sunetta gibberula</i> (Tate)	187	28	3	1
<i>Tawera propinqua</i> (Tenison Woods)	21		1	

No evidence of drilling was found in *Chlamys antiaustralis* (Tate), *Keria johnstoni* (Tate), *Limopsis depressa* (Chapman), *Myadora corrugata* (Tate), *Neotrigonia strangei* (McCoy), *Pleuromeris pecten*, *Scaeoleda* sp., *Tucetona convexa* (Tate).

the preferred sitings of the boreholes, it is possible that predatory naticids used the pronounced umbo of this bivalve to orient themselves to a central position on the valve.

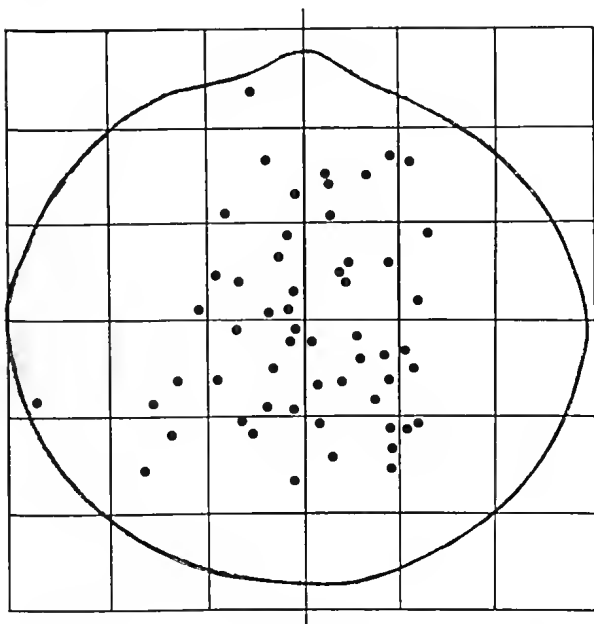


Fig. 2—Scatter diagram for naticid predation on *Glycymeris halli*.

Sunetta gibberula was examined in a similar manner to *G. halli* using an overhead projector to compensate for size differences. This pelecypod has an asymmetric valve and separate scatter diagrams are given for right and left valves (Figs. 3, 4). When the valves were examined it was found that there was a statistically significant preference in the right valve for the side furthest from the umbo. The left valves showed the same ten-

dency with raw data but it was not statistically significant. In view of this, the data from both valves were pooled on a scatter diagram (Fig. 5) and a chi squared test applied to these data. The results show that naticids prefer to drill the side furthest from the umbo ($p < 0.05$). A comparison of observed frequencies of boreholes in the arbitrary quadrats versus a Poisson distribution was also carried out for *S. gibberula* and the result demonstrates that naticids have a preferential site of attack on this bivalve more pronounced than the site preference in *G. halli*. Thus it appears that the asymmetric nature of the valves in this case provides predators with an additional orientation clue above that of the umbo, and that in the case of *S. gibberula* there is a significant tendency to be drilled in the central region of the shell favouring the side furthest from the umbo. Edge drilling was found in only 2% of *G. halli* and *S. gibberula*. On the other hand, Vermeij (1980) found edge drilling to be a significant site of attack by naticids and muricids on recent bivalves in Guam. However, the comparisons between Victorian Tertiary and Recent Pacific deposits is too large a spatial and temporal gulf to expect any correlation.

Because only three muricid bores were found on *S. gibberula* it was not possible to make any statistically meaningful comment upon their distribution; however in all three cases the site of attack was on the side adjacent to the umbo (sites marked "M" in Fig. 5).

The other two species with significant predation percentages, viz. *Placamen subroboratum* and *Notocorbula ephamilla*, did not have sufficient drilled valves to allow any significant results to come from fitting their predation pattern to a Poisson function.

Gastropod predation

Amongst the gastropods, only *Niotha crassigranosa* showed evidence of being a major prey species of other predatory gastropods. The degree of muricid drilling

TABLE 3
PREDATION INTENSITIES ON GASTROPODS AND PELECYPODS IN THE GRANGE BURN COQUINA

Species	% drilled	% naticid	% muricid	% failed
Pelecypoda				
<i>Placamen subroboratum</i>	25	57	7	36
<i>Glycymeris halli</i>	22	82	15	3
<i>Sunetta gibberula</i>	17	88	10	2
<i>Notocorbula ephamilla</i>	15	54	28	18
<i>Ennucula kalimnae</i>	6	90	0	10
<i>Glycymeris</i> sp.	6	100	0	0
<i>Limopsis beaumarisensis</i>	4	100	0	0
Total pelecypod predation intensity (all collected species)	16	75	15	10
Gastropoda				
<i>Niotha crassigranosa</i>	14	50	50	0
<i>Gemmaterebra catenifera</i>	4	100	0	0
<i>Allocospora papillata</i>	2	50	0	50
<i>Polinices cunningghamensis</i>	1	100	0	0
Total gastropod predation intensity (all collected species)	5	70	25	5

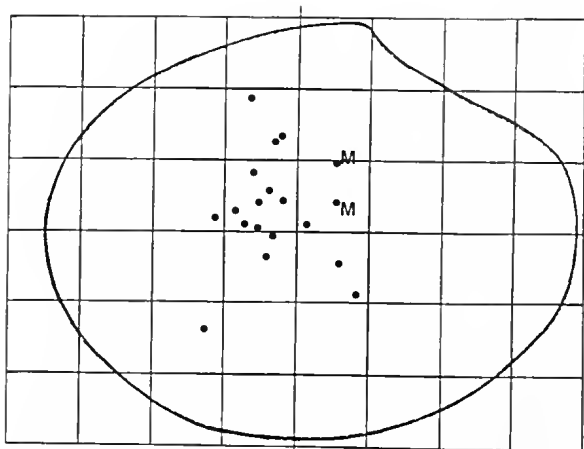


Fig. 3—Naticid predation pattern on right valve of *Sunetta gibberula*.

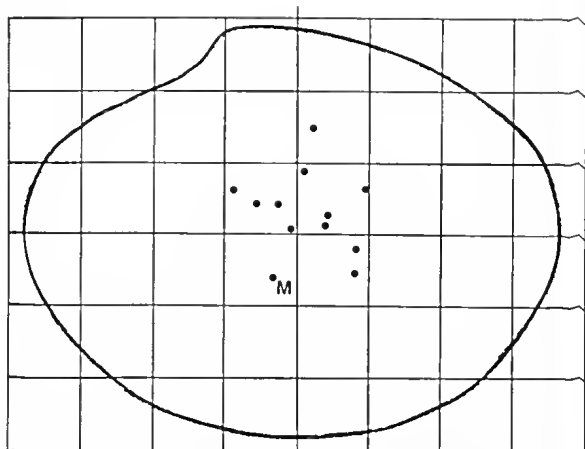


Fig. 4—Naticid predation pattern on left valve of *Sunetta gibberula*.

was high in this species. For both naticids and muricids, in 8 out of 10 cases of drilling, the site was on the penultimate whorl. Adegoke (1974) finds that in the Eocene of Nigeria no preferences can be established for gastropod/gastropod predation despite the fact that gastropods were the favoured predator food source.

Shell texture and drilling frequency

There are conflicting reports in the literature regarding the effect of ornamentation on drilling frequencies in pelecypods. Some authors have pointed to strong external sculpture as a trait that should prevent drilling (Reyment 1967, Taylor 1970). Other authors have found either no relationship (Vermeij 1980, Adegoke and Tevesz 1974), or one that suggests strongly sculptured valves have higher drilling frequencies than do smoother valves (Robba and Ostinelli 1975). Table 4 shows the results from this study. It appears that strong ornamentation is associated with drilling failures. *Placamen subroboratum*, in particular, is a preferred species for naticid attack yet also shows the highest failure rate. Some method of quantifying the degree of ornamenta-

tion (Figs. 6, 7) is needed before any statistical analysis can be done on the relationship between drilling and ornamentation.

TABLE 4
SHELL ORNAMENT AND DRILLING FREQUENCIES

Species	Ornamentation	% Unsuccessful Drills
<i>Placamen subroboratum</i>	Strong lamellae	8.7
<i>Notocorbula ephamilla</i>	Moderate lamellae	2.7
<i>Glycymeris halli</i>	Weak radial ribs—smooth	0.6
<i>Sunetta gibberula</i>	Smooth	0.5

Preference for small prey

A number of investigators (Reyment 1966, Taylor 1970, Adegoke and Tevesz 1974) have concluded that naticids and muricids have a tendency to prey upon the smaller members of a population. Investigation of this concept involves comparing the mean and standard deviation of the drilled sample with the mean and standard deviation of the undrilled population and assessing for significant difference by a Student's *t* test (Table 5). The full calculations for *G. halli* are set out in Appendix 3, including an example of a modified method recommended by Freund (1973, p. 227) when dealing with small samples. In all cases, except *G. halli*, muricid and naticid drilled specimens were pooled to increase sample size. Significant preference was found for smaller bivalves only in *G. halli*; both muricid and naticid predators showing a preference for the juveniles of this species (Table 6). In the other cases, the drilled samples could reasonably be expected from the population by chance, often enough to make the differences of no significance.

CONCLUSIONS

The major predator found in this study was the naticid, *Polinices cumminghamensis*. This gastropod preys preferentially on bivalves, particularly *Placamen*

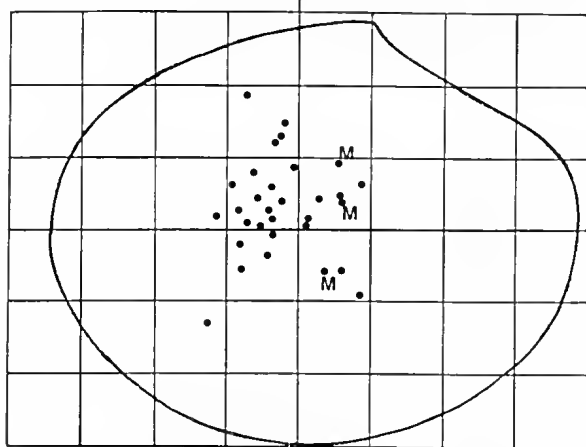


Fig. 5—Combined scatter diagram for *Sunetta gibberula*. Note that muricid bores are marked "M".

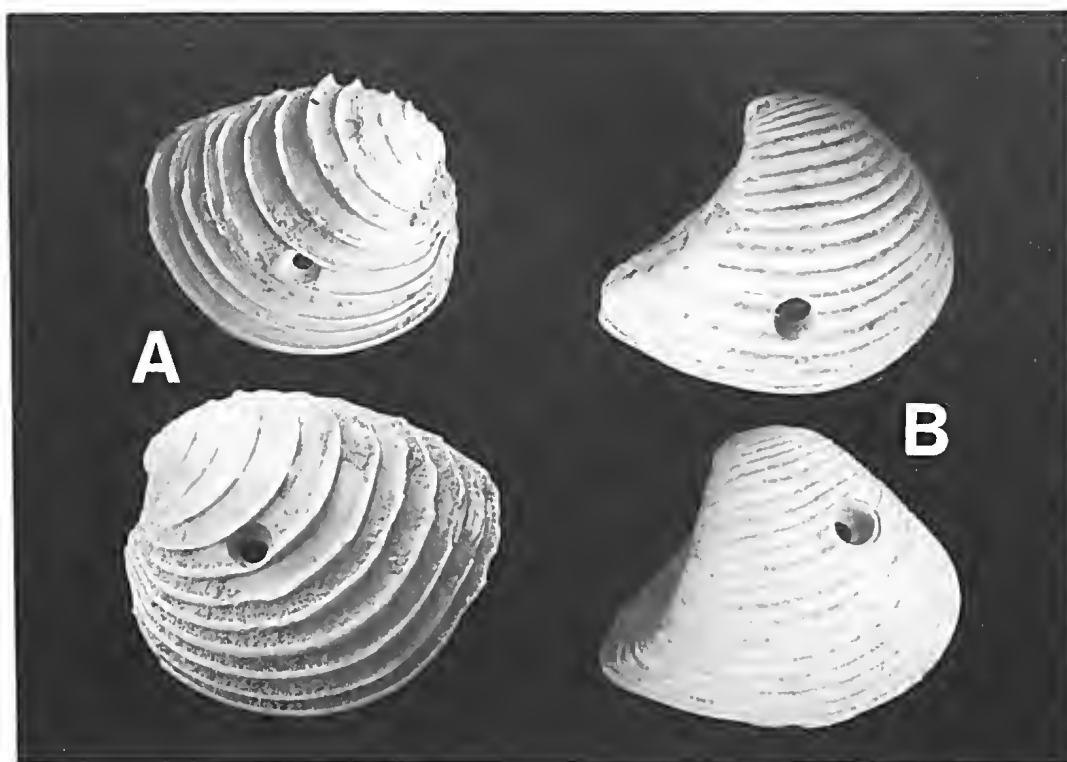


Fig. 6—Gastropod predation in the Grange Burn Coquina. A, *Placamen subroboratum*: Evidence of predation. The valve on the top has one successful and one failed drilling attempt. Note the degree of ornamentation. B, *Notocorbula ephamilla*: above—muricid borehole; below—naticid borehole.

subroboratum, *Sunetta gibberula* and *Glycymeris halli*. The morphology of the holes drilled by this naticid is the typical countersunk paraboloid and is readily distinguished from muricid boreholes. Naticids and muricids were found to prey preferentially on juveniles of the species, *G. halli*, but preferences for juveniles of other species could not be established with confidence. The distribution of boreholes on *G. halli* was not random and the predator possibly used the pronounced umbo of this symmetrical pelecypod to orient itself whilst drilling. No preference was found for either side of the

valve but there was a significant preference for the central area.

The asymmetrical bivalve, *S. gibberula*, was also found to have a preferred area of attack. In this case, there was an even stronger preference for a central region on the opposite side to the umbo. It is possible that the pronounced asymmetrical umbo gives naticids a more specific orientation clue than is the case with *G. halli*.

Shell texture was found to be a significant impediment to successful drilling. The heavily ornamented

TABLE 5
MEAN AND STANDARD DEVIATION OF MAXIMUM DIMENSIONS IN CM OF DRILLED AND UNDRILLED PELECYPODS

Species	Undrilled population			Drilled sample			t value
	n	\bar{x}	s	n	\bar{x}	s	
<i>Glycymeris halli</i> (naticid drilled)	240	1.55	0.36	56	1.38	0.30	3.69
<i>Glycymeris halli</i> (muricid drilled)	240	1.55	0.36	9	1.37	0.21	2.42
<i>Sunetta gibberula</i>	156	2.05	0.30	32	1.98	0.31	1.23
<i>Placamen subroboratum</i>	78	1.85	0.32	26	1.80	0.33	0.65
<i>Ennucula kalinnae</i>	133	1.67	0.16	10	1.64	0.19	0.46

N = sample size \bar{x} = mean s = standard deviation

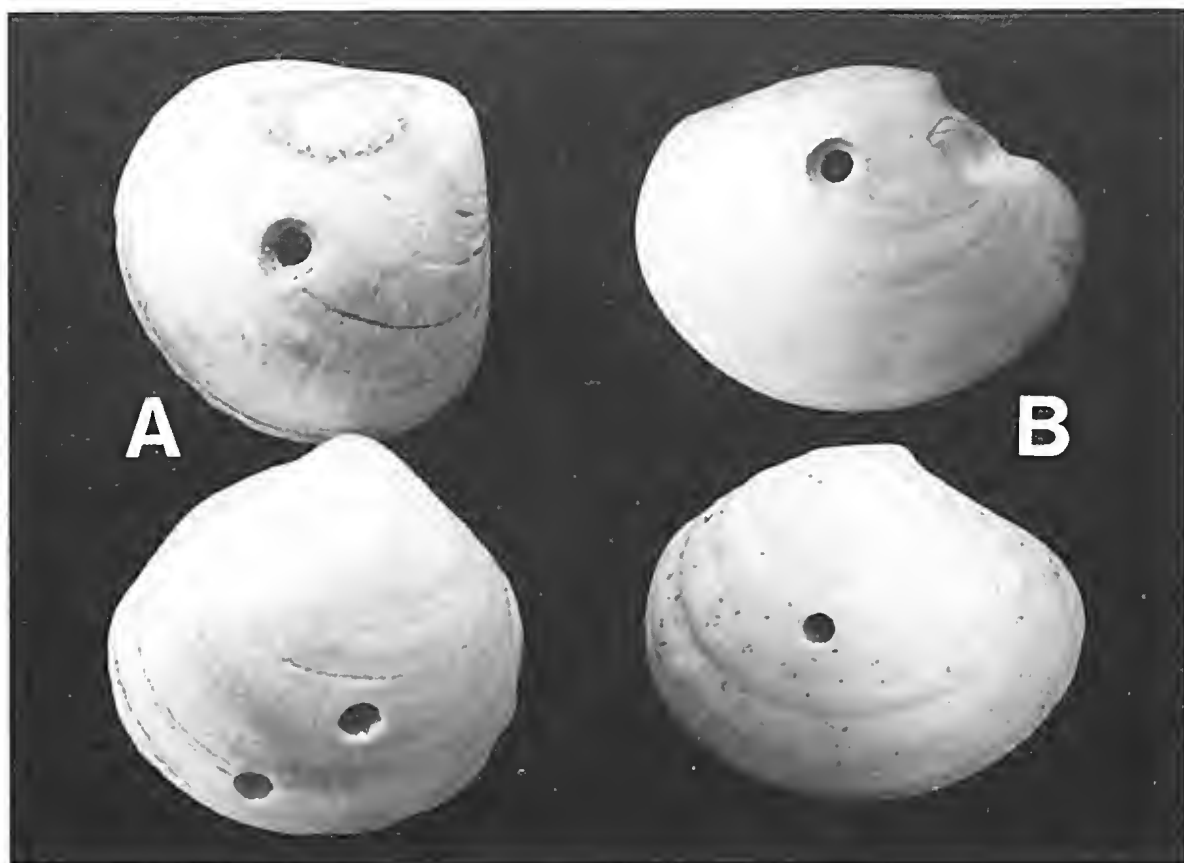


Fig. 7—A, *Glycymeris halli*: above—naticid borehole; below—two successful muricid boreholes on the one valve. B, *Sunetta gibberula*: above—naticid borehole; below—muricid borehole.

pelecypod, *P. subroboratum*, whilst being a preferred prey species, showed a high level of unsuccessful drilling attempts; whilst *S. gibberula*, a smooth pelecypod, provided evidence of very few unsuccessful attacks. Other bivalves of intermediate ornamentation showed corresponding intermediate failure rates.

The main contentious issues in these conclusions are the evidence for ornamentation being a drilling deterrent and that the drills are clustered in particular patterns. The summary presented in Table 7 shows the basic findings from this study compared with those of other

workers using similar materials and methods. The data suggesting preference for small prey are only at variance with the work of Vermeij (1980), and this preference could be more firmly established with a study designed wholly to test the hypothesis with samples large enough to return unequivocal findings. A similar larger sample size would clarify the situation regarding the preferred site of attack. Underpinning all of these attempts at a reconciliation of varying conclusions is the possibility that, given the time and space differences between different studies and their varied faunas, a pattern of

TABLE 6
SIGNIFICANCE OF T TESTS ON DRILLED AND UNDRILLED PELECYPODS

Species	t value	Frequency of t value being obtained by chance	Conclusion
<i>Glycymeris halli</i> (naticid drilled)	3.69	0.001	Significant preference for smaller pelecypods.
<i>Glycymeris halli</i> (muricid drilled)	2.42	0.03	Significant preferences for smaller pelecypods.
<i>Sunetta gibberula</i>	1.23	0.2	No significant preference.
<i>Placamen subroboratum</i>	0.65	0.5	No significant preference.
<i>Ennucula kalimnae</i>	0.46	0.7	No significant preference.

TABLE 7
COMPARATIVE CONCLUSIONS FROM SEVERAL CAINOZOIC MOLLUSCAN PALAEPREDATION STUDIES

Feature	Recent Guam Reef Flats (Vermeij 1980)	Recent Nigerian Shelf (Reyment 1966)	European Eocene (Taylor 1970)	Nigerian Eocene (Adegoke and Eocene 1974)	Victorian Miocene (this study)
Principal predatory bores	murieids	natieids	naticids	natieids	natieids
Incidence of can- nibalism amongst naticids	—	high	high	high	low
Favoured predator food source	bivalves	bivalves	gastropods	gastropods	bivalves
Murieid abundance in assemblage	abundant	abundant	few	rare	rare
Borings concentrated on particular parts of valve in bivalve	—	yes	yes, in naticid borings on gastropods	no	yes
Shell sculpture as a deterrent to boring	no	—	yes	no	yes
Preference for small prey	no	yes	yes	yes	yes, in <i>G. halli</i>

palaeopredation might emerge in each epoch and area which is unique to that time and location. Thus, there may not be a general conclusion to be drawn about preferred sites of attack by naticids on pelecypods but only conclusions which are relevant for a particular fossil assemblage.

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I am grateful for Dr T. A. Darragh of the Museum of Victoria for the time he gave discussing the project and for his work in identifying the fossils collected. My supervisor, Dr K. G. McKenzic, Riverina-Murray Institute of Higher Education, Wagga Wagga, edited the study for publication. Mr R. Lee of Warrnambool took the photographs.

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APPENDIX 1
OBSERVED AND THEORETICAL FREQUENCIES FOR NATICID PREDATION ON *Glycymeris halli*.

Number of holes per square (x)	Observed frequencies (f)	Poisson probability	Theoretical frequencies
0	7	0.101	2.43
1	4	0.232	5.57
2	5	0.266	6.37
3	2	0.203	4.86
4	1	0.116	2.78
5	2	0.053	1.28
6	1	0.020	0.49
7	1	0.007	0.16
8	1	0.002	0.05
	24		23.99

Mean = 2.29 holes per square; variance = 5.69; standard deviation = 2.38; coefficient of variation from a Poisson distribution = 1.04.

CALCULATION OF χ^2 FOR A GOODNESS OF FIT OF NATICID PREDATION ON *G. halli* TO A POISSON DISTRIBUTION.

Number of holes per square	Observed distribution O	Expected distribution E	$\chi^2 = \frac{(O - E)^2}{E}$
0-1	11	8	1.12
2	5	6.37	0.29
3-4	3	7.64	2.81
5 and more	5	1.98	4.61
			$\chi^2 = 8.8$

APPENDIX 2

OBSERVED AND THEORETICAL FREQUENCIES FOR NATICID PREDATION ON *Sunetta gibberula*.

Number of holes per square (x)	Observed frequencies (f)	Poisson probability	Theoretical frequencies
0	23	0.393	11.80
1	2	0.367	11.01
2	1	0.171	5.14
3	0	0.053	1.60
4	2	0.012	0.37
5	1	0.002	0.07
6	0	0.0003	0.01
7	0	0	0
8	0	0	0
9	0	0	0
10	1	0	0
	30		30.0

Mean = 0.93 holes per square; variance = 5.56; standard deviation = 2.36; coefficient of variation from a Poisson distribution = 2.53.

CALCULATION OF χ^2 FOR A GOODNESS OF FIT OF NATICID PREDATION ON *S. gibberula* TO A POISSON DISTRIBUTION.

Number of holes per square	Observed distribution O	Expected distribution E	$\chi^2 = \frac{(O - E)^2}{E}$
0	23	11.80	14.87
1	2	11.07	7.37
2	1	5.14	3.33
3 and more	4	2.05	1.85
			$\chi^2 = 27.42$

APPENDIX 3

STUDENT'S *t* TEST CALCULATION ON *Glycymeris halli*.

Population	Naticid drilled	Muricid drilled
Number (N) $N_p = 240$	$N_n = 56$	$N_m = 9$
Mean \bar{x} $\bar{x}_p = 1.55$	$\bar{x}_n = 1.38$	$\bar{x}_m = 1.37$
Standard deviation s $s_p = 0.36$	$S_n = 0.30$	$S_m = 0.21$

$t = 3.69$ with 239 degrees of freedom.

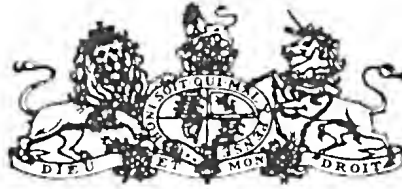
Modified method for smaller samples (Pollard 1968, p. 102).

Example for muricid bored *G. halli* sample.

$$t = \frac{\bar{x}_p - \bar{x}_m}{S_m} \times \sqrt{N-1}$$

$$= \frac{1.55 - 1.37}{0.21} \times \sqrt{9-1} = 2.42$$

$t = 2.42$ with 8 degrees of freedom.



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A REVISION OF *LOLIOLUS* (Cephalopoda; Loliginidae),
INCLUDING *L. NOCTILUCA*, A NEW SPECIES OF SQUID
FROM AUSTRALIAN WATERS

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ABSTRACT: A new species of squid, *Loliolus noctiluca* (Myopsida: Loliginidae) is described and illustrated from Australian waters, the first record of the genus in the region. The genus is revised with complete redescriptions being given for *L. hardwickei* and *L. affinis*. *L. typus* Steenstrup and *L. investigatoris* Goodrich are placed into synonymy with *L. hardwickei*. Natsukari's (1983) synonymy of *Loliolus rhomboidalis* with *Loligo kobienensis* is accepted. *Loliolus steenstrupi* Dall is considered a *nomen dubium*. A key to identification of the valid species of the genus is given. *Loliolus noctiluca* occurs in East Australian coastal waters and estuaries and tolerates salinities as low as 24‰.

During a visit to Australia in 1976, one of us (CFER) first discovered the presence of a species of *Loliolus* in Australian waters in the Sydney Fish Market. Examination of unidentified collections in the Australian Museum, Sydney and the Museum of Victoria, Melbourne confirmed a wide spread distribution of the undescribed species. Many additional specimens subsequently were collected through various field collecting programs. The new species is described and illustrated in this paper.

Loliolus has been an ill-defined genus of loliginid squid considered limited in distribution to the Indian Ocean and eastward into the Indonesian chain. The discovery of a new species in eastern Australian (Pacific Ocean) waters represents a major expansion in the known range both in longitude and latitude. While studying the Australian species it became apparent that a close examination of other nominal species would be necessary in order to make proper comparisons between species. Since most of the original species descriptions are relatively uninformative, especially in view of newly recognized characters, the type specimens were secured and combined with more recently collected material to conduct this revision of the genus.

Loliolus was erected by Steenstrup (1856) to accommodate two new species, *L. typus* and *L. affinis* from the Indian Ocean. Subsequently three additional species have been named: *L. investigatoris* Goodrich, 1896, from the Bay of Bengal; *L. steenstrupi* Dall, 1871, from the Gulf of California; and *L. rhomboidalis* Burgess, 1967, from the Indian Ocean. In this paper *L. steenstrupi* is considered a *nomen dubium* and *L. rhomboidalis*, being placed in synonymy with *Loligo kobienensis* by Natsukari (1983), is removed from the genus *Loliolus*.

MEASUREMENTS AND ABBREVIATIONS

Measurements and indices used throughout this paper are those given in Lu & Tait (1983) and Roper & Voss (1983), using dorsal mantle length (M.L.) as a standard. Fin angle (F.A.) is the angle between the posterior

borders of the fins, this is twice the equivalent measurement used by Roper, Lu & Mangold (1969). Measurements for all specimens are on file in the Department of Invertebrate Zoology, Museum of Victoria. Other abbreviations used include AM—Australian Museum, Sydney; BMNH—British Museum (Natural History), London; CAS—California Academy of Sciences, San Francisco; IM—Indian Museum, Calcutta; NMV—National Museum of Victoria (now Museum of Victoria); NMNH—National Museum of Natural History, U.S.A. (also USNM—U.S. National Museum, used only for catalogue numbers); MUZD—Melbourne University Zoology Department; QM—Queensland Museum, Brisbane; RSMAS—Rosenstiel School of Marine & Atmospheric Science, Miami; ZMC—Zoological Museum, Copenhagen.

Regression analyses and comparisons between regression lines are according to the method given by Zar (1974).

Family LOLIGINIDAE Steenstrup, 1861

Genus *Loliolus* Steenstrup, 1856

TYPE SPECIES: *Loliolus typus* Steenstrup, 1856 (= *Loligo hardwickei* Gray, 1849)

DIAGNOSIS: Loliginids with heart-shaped fins; the entire length of the left ventral arm in males hectocotylied with no normal suckers on the proximal portion of the arm.

Loliolus noctiluca, sp. nov.

Figs. 1, 2, 3a, b, 4-6; Tables 1, 2, 5, 6; Appendices 1, 2

DIAGNOSIS: Largest mantle sucker rings on club smooth; medial mantle suckers 3-6 times the diameter of marginal mantle suckers. No normal suckers on hectocotylied arm (left IV) of males, suckers modified into conspicuous elongate interconnected papillae with minute apical suckers. A pair of photophores embedded in the posteroventral surface of the ink sac.

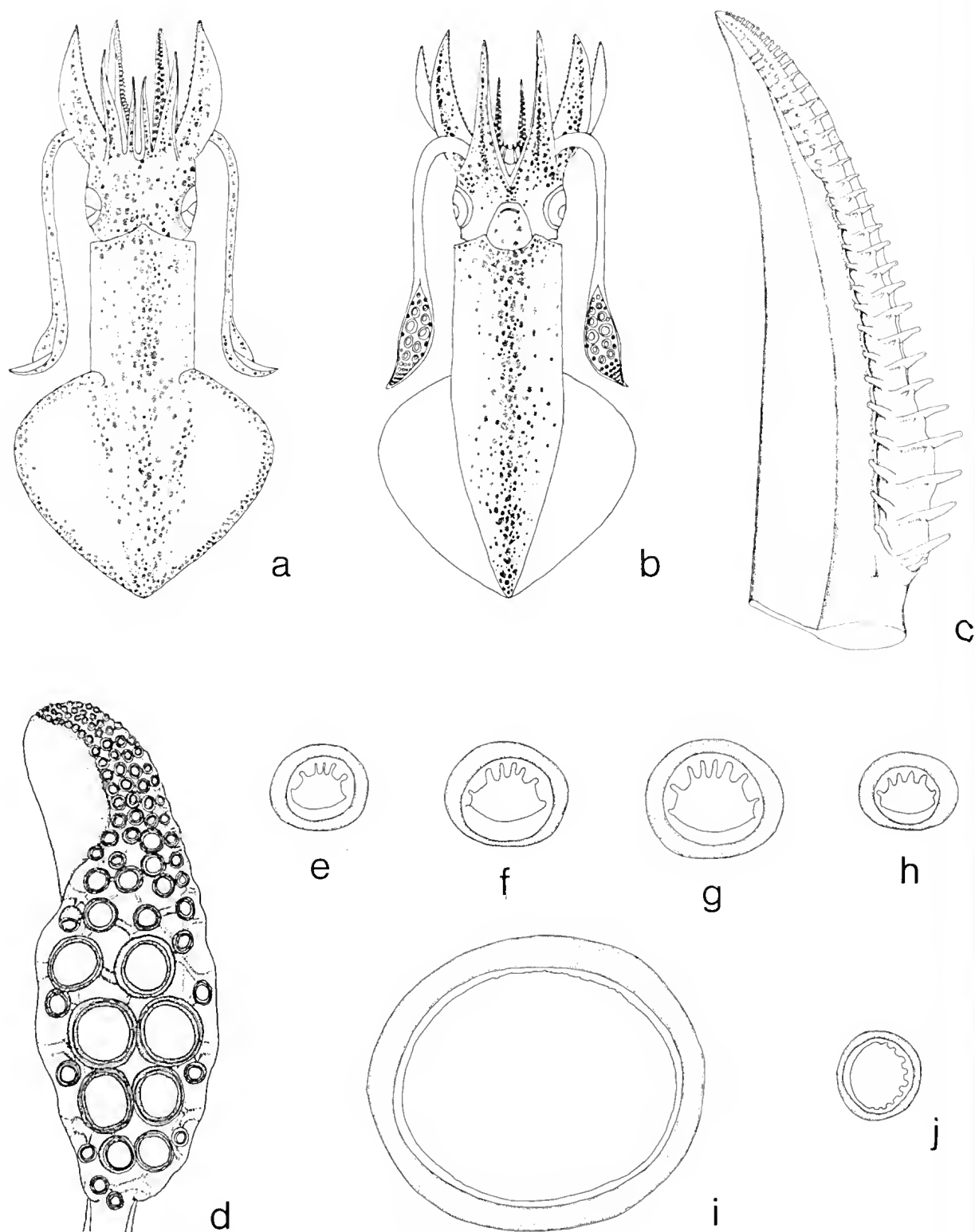


FIG. 1—*Lolilius noctiluca* n. sp. a-b, Holotype NMV F31119, male 59 mm ML. a, dorsal aspect. b, ventral aspect. c, hectocotylus, Paratype NMV F31121, 58 mm ML. d, Left tentacular club of Holotype. e-h, Holotype, largest sucker rings from arms I-IV respectively. i-j, Holotype, club manal sucker rings. i, largest median manal sucker, j, largest marginal manal sucker. (e-j to same scale).

MATERIALS EXAMINED: See APPENDIX 1. Measurements of some additional material (APPENDIX 2) is included in Tables 1 and 2.

DESCRIPTION: *Mantle* cylindrical anteriorly; tapers very gradually posteriorly to a blunt rounded tip; median antero-dorsal lobe rounded, very pronounced; ventrolateral lobes pointed, conspicuous; ventral mantle margin between lobes deeply concave to accommodate large funnel (Fig. 1a, b). *Fins* large, FLI=51-62, FWI=55-76; heart shaped, posterior margins straight, continuous around apex of mantle; anterior margins convex with slightly developed lobes; lateral lobes broadly rounded. Fin length and width indices increase with mantle length. Fins of males longer than females at equal mantle length. The gladius is visible through the integument in the anterior two-thirds of the mantle, then submerges below the muscles of the mantle and fins in the posterior one-third of the mantle.

Head broad, short, as wide as mantle, dorso-ventrally flattened. Eyes large (EDI=11-18), a small pore present between the eye and base of third arm; olfactory apparatus a conspicuous, vertical crest with indentation on posterior side of head. *Funnel* stout, bluntly tapered anteriorly, free in its anterior quarter; funnel and mantle locking cartilage simple, straight groove and ridge, strongly developed. Dorsal funnel organ large;

median limbs very long, broad in posterior half, tapered to a blunt point posteriorly; anterior half of limb narrow; apical papilla simple, subterminal, thumb-like; ventral pads elongate, ovoid, broader anteriorly, medial borders curved, lateral borders nearly straight (Fig. 2a). Funnel valve very well developed, corners rounded, anterior border nearly straight.

Arms short, order III \geq IV, II, I, longer in males than in females, especially Arms I and II. Arm I laterally compressed with a distinct aboral keel for nearly its entire length. Arm II laterally compressed distally, a very low aboral keel present proximally, absent distally. Arm III robust, laterally compressed, a very conspicuous, broad, aboral swimming keel that remains broad well distally. Arm IV trapezoidal in section, very well developed tentacular sheath dorso-laterally, low, angular keel ventro-medially. Protective membranes very broadly developed on all arms except on Arm IV where they are low and weak; trabeculae muscular but do not extend beyond edge of protective membrane on Arms I-III; form scalloped border along membrane of Arm IV. Arm suckers larger in males than females; suckers largest on Arm III and smallest on Arm IV in both sexes (Table 1). *Arm sucker dentition* on chitinous rings of largest suckers on Arms I-III with 4-7 large, truncate teeth in distal half; teeth broad, low laterally,

TABLE 1
MEANS, STANDARD DEVIATIONS, AND RANGES OF SELECTED MEASUREMENTS AND INDICES (IN PER CENT) OF
Loliolus noctiluca n.sp.

Measure/ Index	MALES				FEMALES			
	n	Mean	S.D. (n-1)	Range	n	Mean	S.D. (n-1)	Range
ML (mm)	25			35-62	12			33-83
MWI	25	28.6	1.6	26-31	12	30.0	3.7	26-37
HLI	25	21.9	2.4	17-28	12	23.8	2.2	20-27
HWI	25	28.3	1.3	24-30	12	27.6	2.8	23-34
EDI	25	15.6	0.8	13-17	12	14.7	2.0	11-18
FLI	25	58.3	2.9	51-62	12	54.6	5.7	40-60
FWI	25	67.4	5.2	55-76	12	65.7	5.6	58-74
FL/FW	25	86.9	4.3	78-97	12	83.3	8.2	67-97
FA(°)	25	103.2	4.5	92-111	12	104.9	3.7	96-112
AL _I I	25	22.9	3.1	16-27	12	19.5	4.8	14-32
AL _{II} I	25	34.2	3.2	25-38	12	28.9	5.2	20-42
AL _{III} I	25	38.7	2.6	34-44	12	37.3	4.2	33-49
AL _{IV} I	25	35.6	2.6	31-41	12	35.8	3.6	30-44
HcAI	23	38.1	2.7	32-44	—	—	—	—
TtLI	25	73.1	10.4	60-106	12	81.2	19.9	55-136
CILI	25	28.9	2.6	25-36	12	31.8	3.6	28-41
AS _I I	25	0.61	0.09	0.5-0.8	12	0.52	0.09	0.4-0.7
AS _{II} I	25	0.79	0.10	0.5-1.0	12	0.66	0.08	0.5-0.8
AS _{III} I	25	0.86	0.10	0.7-1.1	12	0.80	0.09	0.7-0.9
AS _{IV} I	25	0.54	0.08	0.5-0.8	12	0.48	0.08	0.3-0.6
CISI	24	2.25	0.31	1.7-2.8	11	2.58	0.45	2.0-3.4
GW	22	21.3	1.3	18-23	11	22.7	1.8	20-26
RLI	5	17.4	1.5	15-19	5	18.2	1.9	16-20
RWI	5	4.48	0.44	3.8-4.8	5	4.87	0.33	4.4-5.2
SpL(mm)	17	4.15	0.64	3.2-5.2				
SpLI	17	7.74	0.90	5.6-9.3				
SpRI	17	81.2	3.6	73-87				
SpWI	17	4.36	1.50	3.1-7.8				

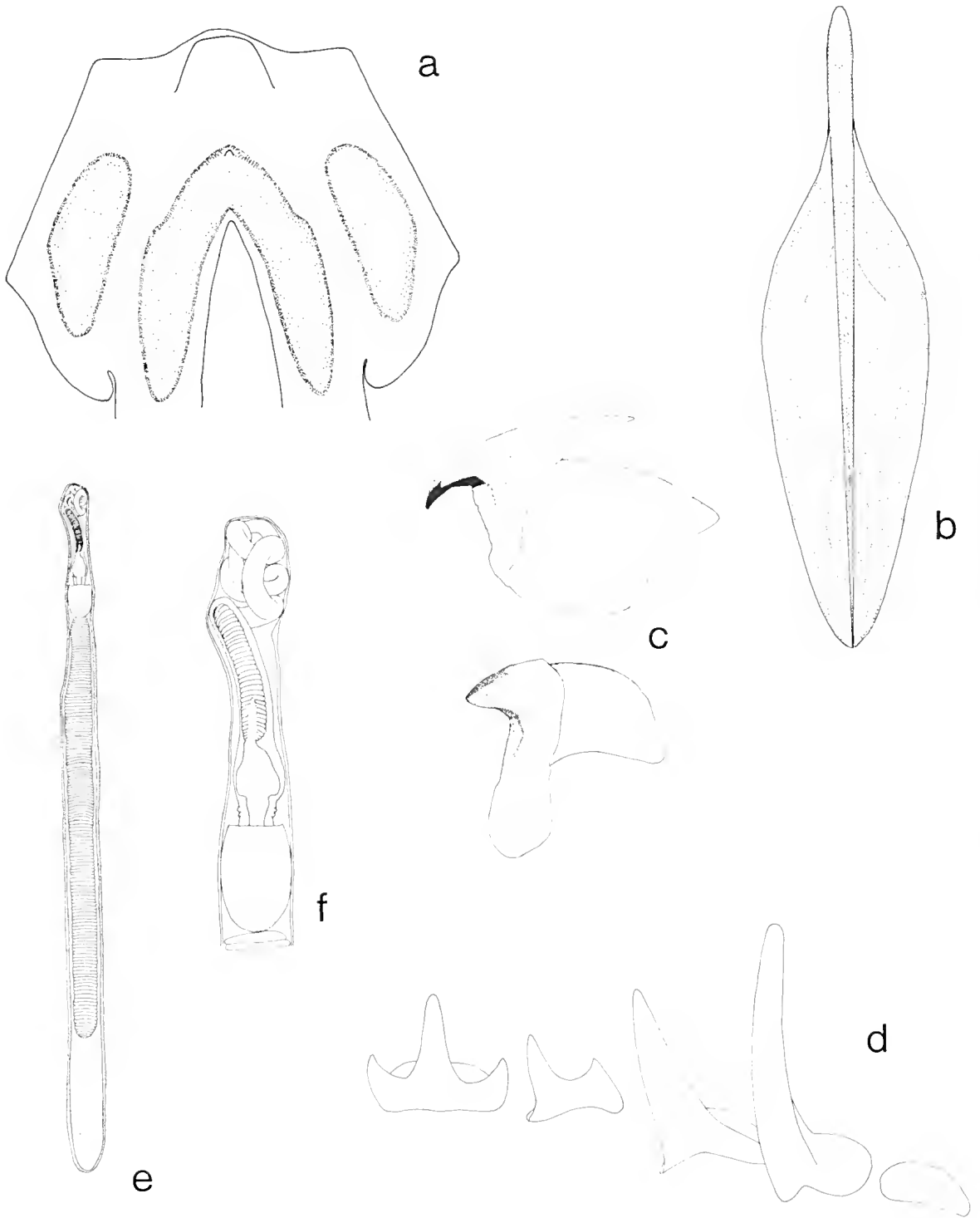


FIG. 2—*Loliolus noctiluca* n. sp. a, Paratype NMV F31122, male, 62 mm ML, funnel organ. b, Paratype NMV F31120, male, 60 mm ML, gladius. c, NMV F31130, female, 60 ML, beaks. d, Paratype NMV F31122, radula. e-f, Paratype NMV F31120. e, spermatophore. f, oral end of spermatophore.

narrow, elongate medially (Fig. 1e,f,g); proximal half a broad, smooth plate. Ring of largest sucker on Arm IV (Fig. 1h) with 3-6 teeth, similar to those on Arms I-III. Distal-most sucker rings with more rounded teeth, generally fewer than those on largest rings. Right ventral arms of males from Queensland and Papua have sucker rings with 3-6 acute, pointed teeth on the distal 31-36 pairs of suckers, with blunt teeth on the remaining proximal 3-9 rows. Females show no corresponding difference.

Left ventral arm of males is *hectocotylised* (Fig. 1c), and is longer, more robust than right ventral arm. All suckers are modified. Armature of ventral row with suckers and stalks modified into long papillae that become shorter and more robust distally; a thick membrane connects the medial bases of the ventral papillae on the proximal two-thirds of the arm and continues to the tip as a low ridge. Suckers of ventral row are small, swollen and fleshy and distally are incorporated into the papillae as slightly swollen tips. Minute, chitinous sucker rings are deeply embedded in the swollen suckers on the proximal portion of the ventral row. Suckers and stalks of dorsal row are modified into shorter and narrower papillae, that distally decrease in length to very small, conical protuberances; dorsal papillae along basal half are fused by a narrow membrane to the medial membrane between the papillae of the ventral row. Suckers of the proximal portion of dorsal row are bulbous with small apertures and the most proximal, at least, possess minute rings. As papillae decrease in size

and become conical, suckers are completely incorporated into the apex of the papillae, and a minute orifice remains to the distal-most papillae. The ventral protective membrane is thicker and wider than that of the right ventral arm; it becomes broader along the distal half of the arm before it tapers to the tip. The dorsal protective membrane originates proximally as a thick, broad, semi-lunar flap with a swollen, convoluted medial surface. A fleshy, convoluted papilla arises from the base of the most proximal sucker stalk. The most proximal section of the ventral protective membrane also is thickened and convoluted. Proximal to the semi-lunar flap, the dorsal protective membrane is thin and narrow with a scalloped border. On the distal third of the arm, the dorsal protective membrane becomes a broadly expanded, thickened flap with a fleshy convoluted medial surface.

Tentacles relatively short, robust; stalks naked and with large, broadly expanded clubs, $CL_1=25-40$ (Fig. 1d). Club suckers tetraserial on manus and dactylus; carpal structures absent; manal suckers in 6-7 rows, large and distinct from dactylus suckers; median 6-8 suckers of manus greatly enlarged (0.8-0.2 mm diameter), 3-6 times the diameter of marginal suckers. Dactyl suckers in 15-18 tetraserial transverse rows, grading to minute distally; no distal circle of minute dactyl suckers exists. Protective membranes arise at the proximal end of the club and expand rapidly to broad sheaths. The marginal rows of suckers on the manus lie

TABLE 2
COMPARISON OF MORPHOLOGICAL PARAMETERS SHOWING SEXUAL DIMORPHISM IN *Loliolus noctiluca*
Regression data relating to Fig. 5. $y = bx + a$; b = regression coefficient; a = vertical intercept; r = correlation coefficient; p = significance of the regression line; n = sample size; sig. diff. = significant difference between the regression lines of males and females, with respect to slope or elevation.

Ref. Fig. 5	y	:	x	Sex	n	b	a	r	p	sig. diff.
a	HL	:	ML	♂	25	0.181	2.018	0.70	$p < 0.001$	$p < 0.05$ (elev.)
				♀	12	0.199	1.880	0.94	$p < 0.001$	
b	ED	:	ML	♂	25	0.142	0.724	0.91	$p < 0.001$	$p < 0.05$ (slope)
				♀	12	0.088	2.914	0.83	$p < 0.001$	
c	FL	:	ML	♂	25	0.682	-5.109	0.96	$p < 0.001$	$p < 0.005$ (elev.)
				♀	12	0.693	-7.194	0.99	$p < 0.001$	
d	GW	:	ML	♂	22	0.180	1.662	0.87	$p < 0.001$	$p < 0.05$ (slope)
				♀	11	0.251	-1.176	0.97	$p < 0.001$	
e	AL _I	:	ML	♂	25	0.313	-4.340	0.80	$p < 0.001$	$p < 0.05$ (elev.)
				♀	12	0.273	-3.844	0.85	$p < 0.001$	
f	AL _{II}	:	ML	♂	25	0.380	-1.928	0.84	$p < 0.001$	$p < 0.001$ (elev.)
				♀	12	0.369	-3.930	0.90	$p < 0.001$	
g	CL	:	ML	♂	25	0.303	-0.749	0.83	$p < 0.001$	$p < 0.02$ (elev.)
				♀	12	0.291	1.367	0.89	$p < 0.001$	
h	AS _I	:	ML	♂	25	0.0082	-0.1103	0.74	$p < 0.001$	$p < 0.01$ (elev.)
				♀	12	0.0067	-0.0750	0.92	$p < 0.001$	
i	AS _{II}	:	ML	♂	25	0.0094	-0.0808	0.75	$p < 0.001$	$p < 0.002$ (elev.)
				♀	12	0.0076	-0.0520	0.93	$p < 0.001$	
j	CS	:	ML	♂	24	0.0318	-0.4804	0.80	$p < 0.001$	$p < 0.05$ (elev.)
				♀	11	0.0206	-0.2636	0.75	$p < 0.001$	

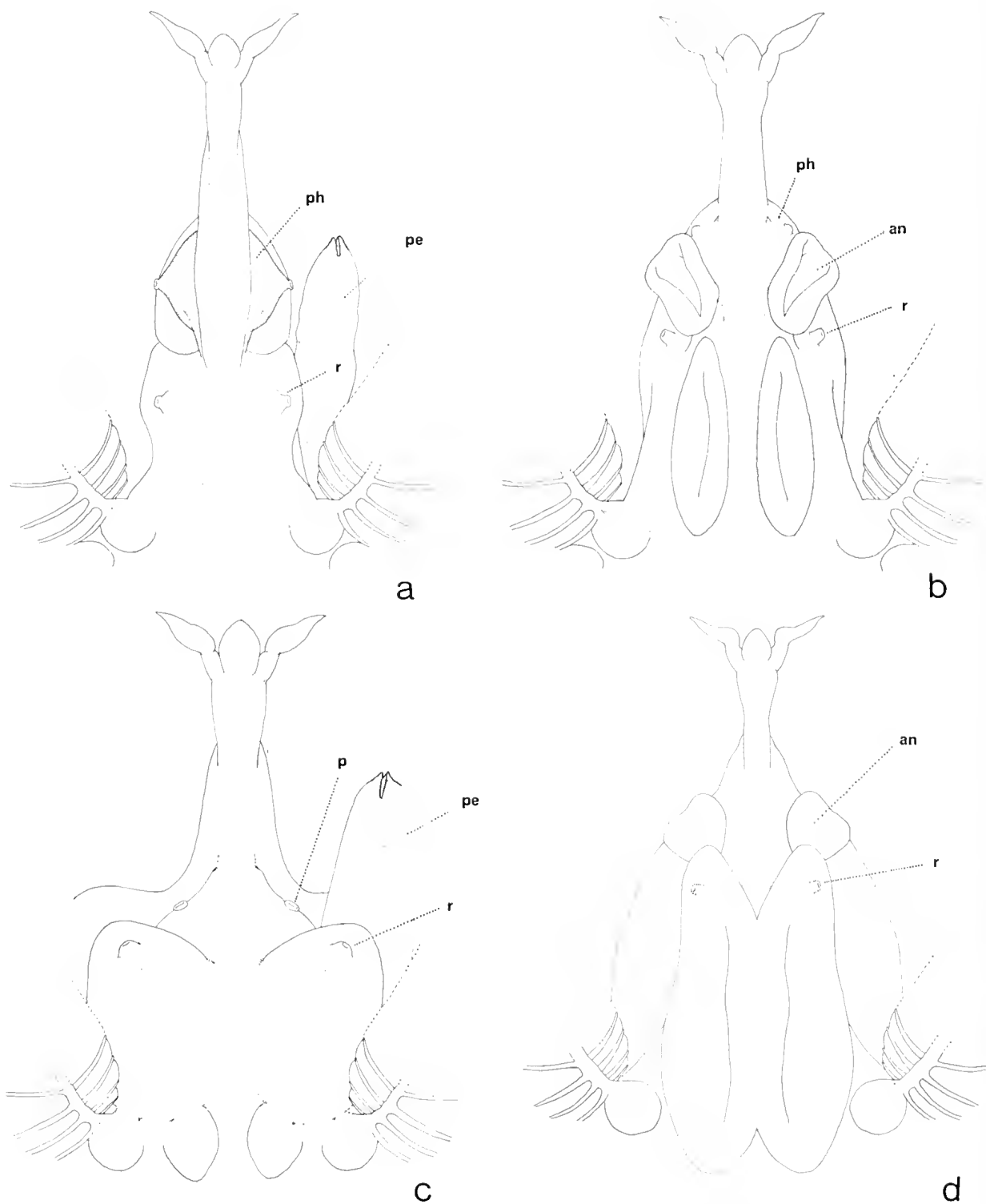


FIG. 3—Ventral views of the visceral mass. a, *Lololus noctiluca*, male (Paratype, NMV F31121, 58 mm ML). b, *Lololus noctiluca*, female (Paratype, NMV F31123, 33 mm ML). c, *Lololus hardwickei*, male (ZMC, 29°18'N, 50°27'E, 49 mm ML). d, *Lololus hardwickei*, female (ZMC, 29°18'N, 50°27'E, 53 mm ML). Abbreviations: ph, photophore. pe, penis. p, papilla. r, renal opening. an, accessory nidamental gland.

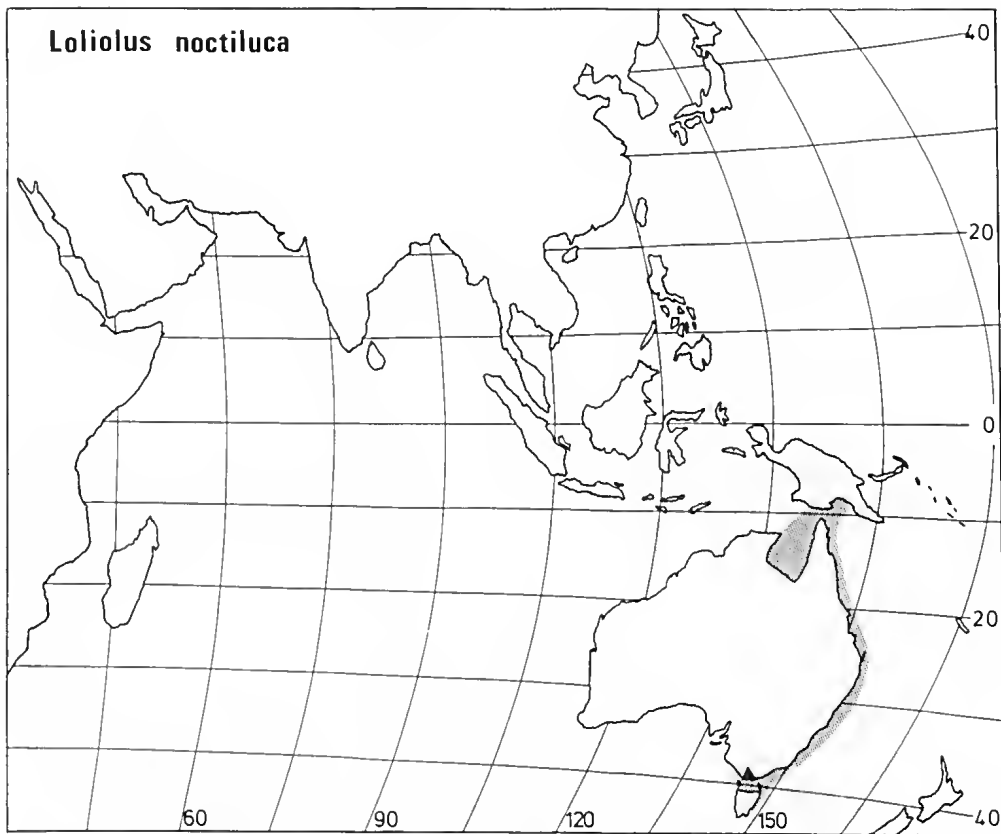


FIG. 4—Distribution of *Loliolus noctiluca* n. sp. Shaded area shows general distribution, solid triangle indicates type locality.

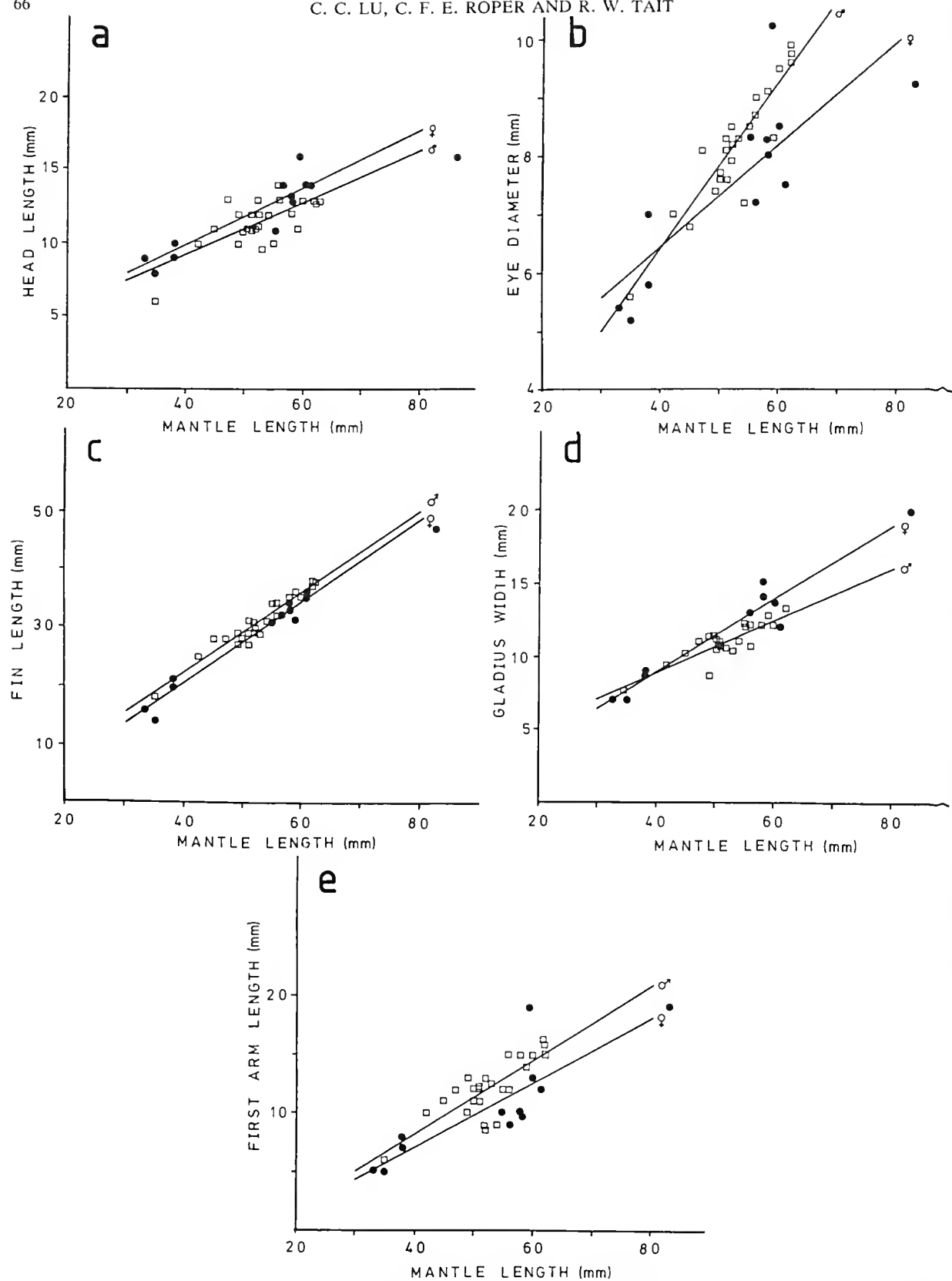
on the expanded protective membrane; sucker stalks arise distally from the broad trabeculae. The protective membranes narrow markedly along the dactylus; the ventral one extends to the tip of the dactylus and the dorsal one terminates along the proximal half of the dactylus. The swimming keel arises on the aboral angle of the club at a point in line with the fourth to fifth row of manal suckers. It expands very rapidly and becomes considerably broader than the oral surface of the dactylus (ratio of 3:2), then terminates abruptly at the tip.

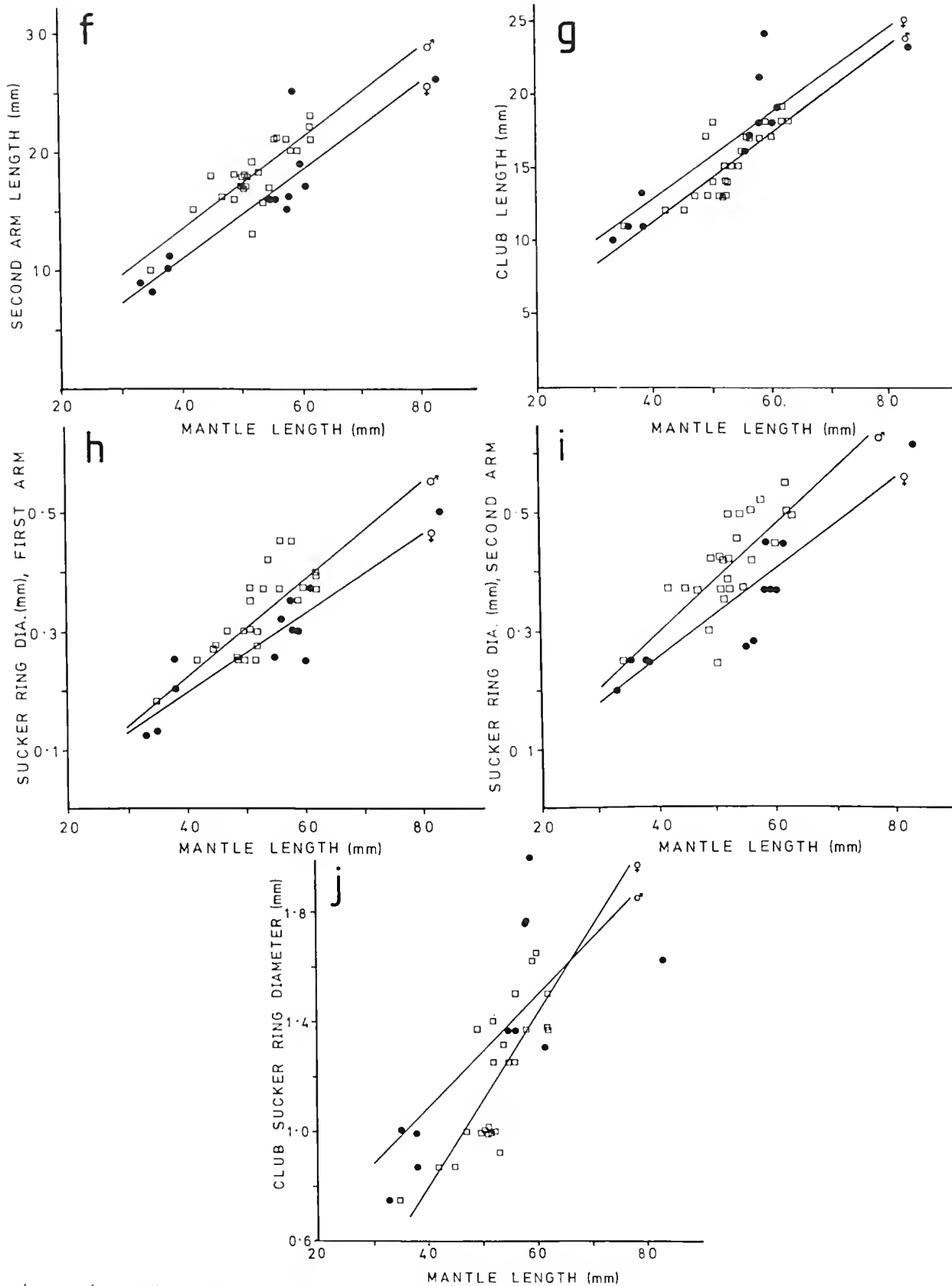
Club sucker dentition (Fig. 1i,j) includes proximal-most suckers with chitinous rings that possess very low, rounded to truncate teeth around entire ring; largest distally, minute proximally. Median manal suckers larger in females than males (see Table 1 and Section on "Sexual dimorphism"). Rings of medial manal suckers with numerous, broad, extremely low (so low that margin appears smooth or finely scalloped), plate-like teeth distally, becoming lower and narrower laterally and barely distinguishable proximally. The outer soft rings with minutely granular sculpture. Lateral manal sucker rings with 10-12 very small, low, truncate to rounded, teeth in the distal half; proximal half to two-thirds smooth. The exterior margin of manal suckers bears numerous, short ribs around entire margin giving plated appearance. Dactyl sucker rings with 20-30 spaced, small, truncate to rounded teeth around entire margin; longer and narrower distally, grading to shorter

and broader laterally, and minutely emarginate to smooth proximally.

Lappets of *buccal membrane* with 0-6 suckers each, dentition lacking; sucker sizes vary greatly even on individual lappets. Females bear a small buccal seminal receptacle on the convoluted oral surface of the buccal membrane between the ventral lappets. *Gladius* (Fig. 2b) broad (GW 18-26), slightly more so in females. Vane very thin, strongly curved posteriorly, widest in its anterior third; without thickenings. Free rachis short and narrow (RL 15-20, RW 3.8-5.2), median groove rounded, shallow; lateral rods weak.

Upper beak (Fig. 2c) with sharply pointed, long, curved rostrum; width slightly greater than length; rostral margin and tip brown to black, remaining area of rostrum and hood light brown (varies with age and state of preservation). Hood length about three-quarters of crest length; wing length about 1.5-2.0 times rostral length, cutting edge of wing irregular, no notch or prominent tooth present. Crest curved, lateral wall large, pigmented anteriorly, posterior margin with a deep indentation; margins of wing, hood, crest and lateral wall transparent. **Lower beak** (Fig. 2c) with short, pointed rostrum; light yellowish brown except near jaw angle and outer margin of rostrum which are dark reddish brown; cutting edge of rostrum straight, irregularly serrated, rostral width equal or slightly less than rostral length. Hood short, about twice rostral length, wing

FIG. 5—Sexual dimorphism in *Loliolus noctiluca* n. sp. For regression formulae



and comparison of lines, refer to Table 2. Open squares—males. Solid dots—females.

length about three times rostral length, cutting edge of wing straight, irregularly serrated; club-shaped darkened area at centre of wing; entire margin of hood and wing transparent. Crest curved, crest length about four times rostral length; lateral wall length about five times rostral length, light brown at centre, transparent around margins. *Radula* (Fig. 2d) with seven transverse rows of teeth; rachidian tooth slender with sharp curved lateral cusps; first lateral tooth long with a sharp lateral cusp; second lateral tooth straight, without cusps; third lateral tooth straight to slightly curved with broad lateral expansion; marginal plates small, oblong.

Spermatophores (Fig. 2e,f) small (SLI 5.6-9.3); sperm mass comprises 73-87% of length. Aboral part of cement body long, barrel-shaped, oral part flask shaped, connected to aboral part by a short neck. Middle tunic spirally sculptured opposite oral part of cement body, with a single groove around it opposite the neck. Oral dilation of the spermatophore contains several coils of the ejaculatory apparatus. The site for attachment of spermatophores on mature females is on the ventral buccal lappets, adjacent to the buccal seminal receptacle. On females in spawning condition, the spermatophores may be attached to a glandular patch or spermatophore pad on the ventro-lateral surface of the left funnel adductor muscle, adjacent to the opening of the oviduct.

Colour in isopropyl alcohol cream, with large brown to dark maroon chromatophores distributed evenly over mantle, head and aboral surface of arms; chromatophores on dorsal surface of mantle and head usually larger and more concentrated than on ventral surface. A narrow band of very concentrated, small chromatophores borders free dorsal margins of fins; a large semilunar patch devoid (or nearly so) of chromatophores lies medial to the chromatophore band on each fin. A broad band of large, very concentrated chromatophores extend along dorsal midline of fins. The ventral surfaces of fins are devoid of chromatophores. A pair of oval *photophores* (Fig. 3a,b) lie embedded in the postero-ventral surface of the bulbous ink sac, one photopore on each side and slightly dorsal to the intestine that lies ventral to and fused with the ink sac and duct. Each photophore has a short, conical, postero-ventrally directed papilla with a minute, recessed orifice; these lie in line with and anterior to the renal papillae. The major portion of each photophore is a large, swollen, bulb that lies deeply embedded creating a deep pit in the ink sac. A heavy sheath of bronze-coloured, reflective tissue backs the photophores and separates them from the ink sac. No duct or connection appears to exist with the ink sac other than that caused by the membranes that bind the photophores to the sac. The tissue of the photophore is cream-coloured, granular and convoluted. In fully mature females the anterior tips and openings of the swollen nidamental glands lie immediately ventral to the papillae, while the single oviduct and oviducal gland (accessory nidamental gland) opens just postero-dorsal to the papilla on the left side. In general the photophores are reminiscent of the type described in *Uroteuthis bartschi* (Haneda 1963).

SIZE AT MATURITY: Spermatophores occur in males as small as 40 mm ML and the nidamental glands of females begin enlargement at a similar size. All specimens larger than 50-60 mm ML were completely mature. The largest specimen examined was a female of 83 mm ML and the largest males were 62 mm ML.

Comparison of the two series from northern Port Phillip Bay (NMV F31119-F31122, F31130, F31200, F31211, USNM 813798 and USNM 813974, USNM 813977) taken in October and February respectively, shows no reproductive seasonality (Fig. 6). Animals in both samples matured at similar sizes, although mature females generally were larger than mature males. In the October sample the ratio of males to females was 10.5:1, while in the February sample it was 1.1:1. We have insufficient material to allow an interpretation of these widely variant sex ratios.

HOLOTYPE: 59 mm, mature male; National Museum of Victoria, No. F31119.

TYPE LOCALITY: Northern Port Phillip Bay, Victoria, Australia, 37°53'S, 144°50'E, 9 m. Sandy bottom with scattered patches of sea grass.

DISTRIBUTION: Inshore waters, mainly bays and estuaries, on East and Southeast Australian coasts, including Tasmania (42°56'S) to the Gulf of Papua (7°57'S) and Gulf of Carpentaria (Fig. 4). Taken in bottom trawls and beach seines from 0-46 m.

Loliolus noctiluca is the only member of its genus known in Australian waters. Previously, the easternmost record for the genus was that of *L. investigatoris* from Java (Adam 1954).

ETYMOLOGY: The specific name *noctiluca* (that shines at night, the moon) refers to the presence of photophores on the ink sac as well as to the semilunar patches devoid of chromatophores on the dorsal surface of the fins.

REMARKS: *Sexual dimorphism.* Although there is no obvious secondary sexual dimorphism in *Loliolus noctiluca*, there are a number of statistically significant morphometric differences between sexes (Fig. 5), statistical comparisons between sexes are given in Table 2. The first and second pairs of arms are longer and their suckers generally larger in males than in females. This is not evident in the third pair of arms, and the fourth pair shows differences only in the diameter of the sucker rings ($p < 0.05$). The club length and diameter of the largest anal sucker rings are greater in females; head length of females also is greater but no difference in head width is apparent. Males have slightly larger fins than females at all sizes.

In all the above, differences between regressions are with respect to elevation only. However, gladius width and eye diameter both show different growth rates between sexes (Fig. 5b, d), which may result in marked dimorphism at larger sizes.

SALINITY TOLERANCE: *Loliolus noctiluca* has been taken in estuarine waters with bottom salinities as low as 24‰ and surface salinities as low as 17.5‰, at temperatures of approximately 11°C (J. Beumer pers.

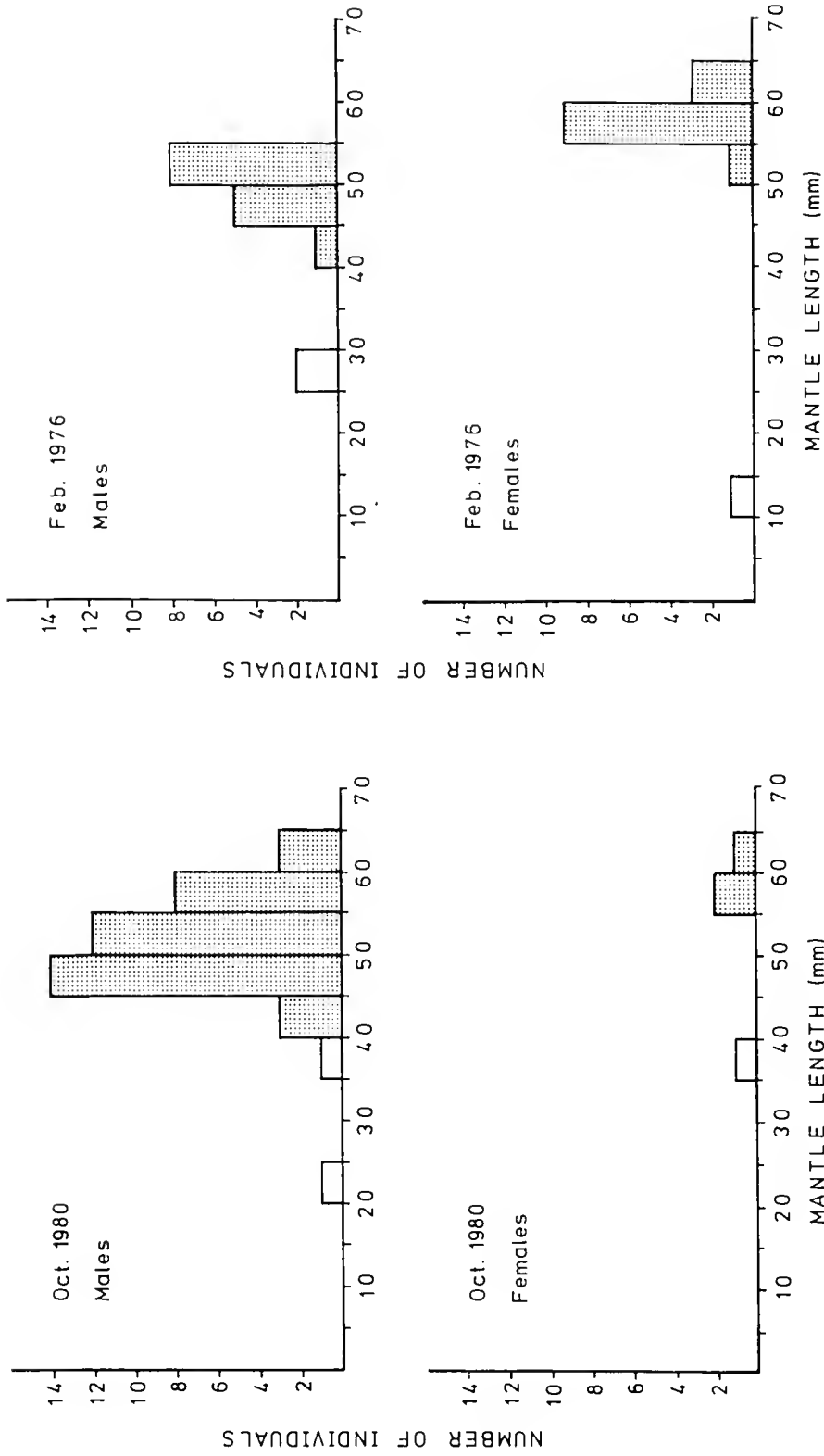


FIG. 6.—Size frequency distributions of two samples of *Lolius noctiluca* n. sp. from northern Port Phillip Bay, Victoria. October sample, n = 46. February sample, n = 30. Shaded areas represent sexually mature specimens.

comm). The tolerance of low salinity is unusual for a cephalopod. The only other cephalopod known to withstand less saline waters is *Lolliguncula brevis* from the southeastern United States, where it has been recorded at salinities as low as 17‰ (Dragovich & Kelly 1967, Gunter 1950). *Lolliguncula tydeus* also has been reported from brackish waters, but its exact salinity tolerance is not known (Brakoniecki 1980).

GEOGRAPHIC VARIATION: Two distinct forms of *Loliolus noctiluca* exist on the East Australian coast. Animals from the inshore waters of Bass Strait have blunt or irregular teeth on the suckers of the fourth right arm of males. Males from Queensland to Papua have acute, pointed teeth on the distal 31-36 rows of suckers, with blunt teeth on the proximal 3-9 rows. This difference is not shown in females, nor do any other corresponding morphological differences appear in males. Detailed examination of the spermatophores shows them to be identical between forms. Therefore there is no justification for separate specific or subspecific status for the two forms.

***Loliolus hardwickei* (Gray, 1849)**

Figures 3c,d, 7, 8; Tables 3, 5, 6

Loligo hardwickei Gray, 1849, p. 69; Nesis, 1982, p. 132.

1856 *Loliolus typus* Steenstrup, p. 194, pl. 1, fig. 5, 5'.

1896 *Loliolus investigatoris* Goodrich, p. 8-9, pl. 2, figs. 29-37.

1916 *Loliolus investigatoris*, Massy, p. 222.

1939 *Loliolus investigatoris*, Adam, p. 66, fig. 1.

1954 *Loliolus investigatoris*, Adam, p. 129, figs 2-4.

1968 *Loliolus typus*, Silas, p. 307.

1968 *Loliolus investigatoris*, Silas, p. 307; Nesis, 1982, p. 132, fig. 34a, b, v, g.

MATERIALS EXAMINED: See APPENDIX 3.

DESCRIPTION: *Mantle* (Fig. 7a) stout (MW1 27-53), slightly dorso-ventrally flattened, mantle wall thin, body tapers evenly from about one-third of its length to posterior tip; antero-dorsal lobe conspicuous, rounded; ventro-lateral lobes low, pointed; gladius visible through body wall in mid-dorsal line for almost entire length. *Fins* together heart shaped, occupy 51-71% of mantle length, width greater than length (Table 3); fins continuous around posterior end of body, posterior margins straight, anterior margins convex. *Funnel* small, locking apparatus normal, *valve* terminal, slightly rounded; *dorsal funnel organ* with lateral limbs stout posteriorly, posterior ends rounded, limbs much narrower anteriorly, apex slender, acutely pointed, small blunt apical papilla present; ventral pads ovoid, stout, half to two-thirds of length of dorsal organ. Head and eyes large (Table 3), olfactory crest low, preocular pore present adjacent to base of third arm.

Arm order generally III, IV, II, I (III, II, IV, I in type); Arm I very short, laterally compressed, low aboral keel present for entire length; Arm II slightly compressed distally, low aboral keel present for entire length; Arm III robust, broad, dorso-ventrally compressed, well developed aboral keel present for entire

length, widest at proximal one-third; Arm IV not compressed, trapezoid in section, narrow tentacular sheath present dorsally, low flange present on entire length ventro-medially. Trabeculate protective membranes on Arms I-III well developed, margin generally straight, trabeculae weak, form high points along membrane edges in some specimens; membranes on Arm IV lower than on other arms, trabeculae weak, form high points along edge of membrane. *Suckers* largest at about half arm length, larger in males than in females (Table 3), diminish evenly to become minute at tip. Suckers in ventral rows on Arms II and III of males only similar in size to those in dorsal row but with smaller apertures, giving the ventral suckers a globose appearance; apertures of ventral suckers 0.6-0.9 times diameter of dorsal suckers. *Arm sucker dentition* shows sucker rings of the largest suckers on Arm I with 3-5 large, rounded trapezoidal teeth on distal and lateral margins, proximal plates smooth, low; suckers on Arms II and III in females and dorsal sucker row of males (Fig. 7d) with 3-7 low, square or trapezoidal teeth on distal and lateral margins, proximal plates very low; ventral suckers of Arms II and III in mature males (Fig. 7e) with only 2-4 large trapezoidal teeth on distal and lateral margins, proximal plates higher than those in the dorsal row; Arm IV with 2-5 low, square or trapezoidal teeth similar to those on Arm I.

Left ventral arm of males *hectocotyliised* (Fig. 7b), slightly shorter and slimmer than the right ventral arm (Table 3), usually curved orally in preserved specimens. Suckers entirely absent, sucker stalks of ventral row entirely absent or entirely fused with the ventral trabeculate membrane; ventral membrane greatly enlarged and thickened into a fleshy ridge, proximal 2-3 trabeculae further enlarged to twice the height of the rest of the membrane, inclined slightly distally to form a proximal fleshy crest, distal to this crest the membrane diminishes evenly to tip, 2-3 minute normal suckers present at distal tip; trabeculae all broad, nearly joining, fused together for entire length by the thick, fleshy connecting membrane. Dorsal sucker row reduced to minute free papillae, not fused to the protective membranes; papillae opposite the proximo-ventral crest often enlarged, decline evenly to distal tip, 2-3 minute normal suckers at tip; dorsal protective membrane normal, fused at proximal origin to ventral membrane, low, edges may be scalloped for some of its length, declines evenly to distal tip; trabeculae weak. The proximal crest on the ventral membrane, the total lack of suckers and the curve of the arm in preserved specimens combine to give the hectocotylus a sickle-like appearance.

Tentacles short, slender, stalks naked, clubs small, only slightly expanded, CLI 22-38 (Fig. 7c); carpal suckers biserial for first 1-2 rows, other suckers on club arranged tetraserally; dactylus slender, distinct from manus; manal suckers in about 7 rows, median suckers 1.0-1.3 times diameter of marginal suckers; dactylus suckers small, only slightly larger in ventral row, suckers diminish to minute distally. Trabeculate protective membranes arise along proximal portion of carpus; low,

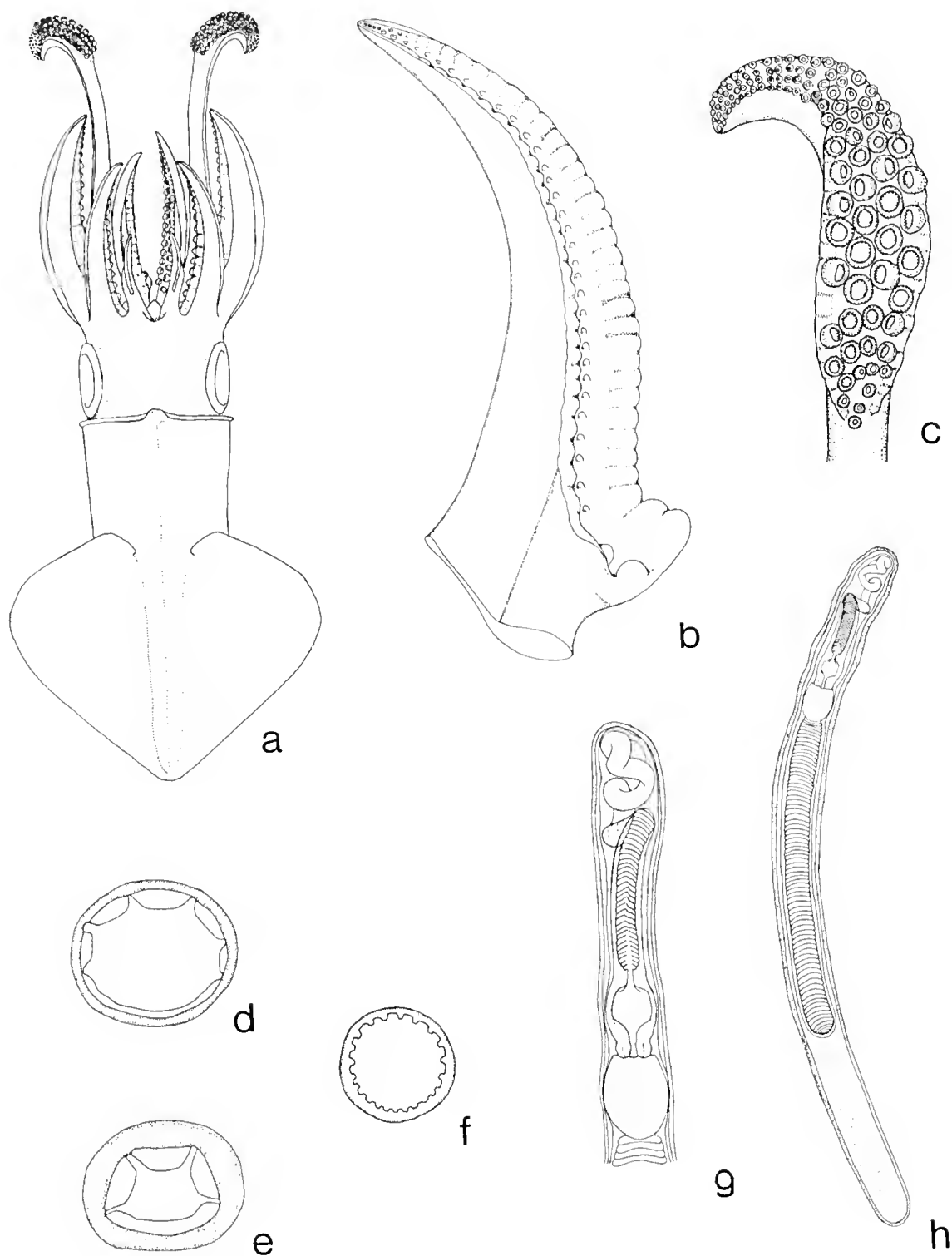


FIG. 7—*Loliolus hardwickei* (Gray), IM $\frac{3646}{7}$, male 33 mm ML. a, dorsal view. b, hectocotyliised arm. c, left tentacular club. d, largest sucker ring from dorsal row of the third arm. e, sucker ring from the ventral row in same pair as (d) (d and e to same scale). f, largest club median anal sucker ring. g, oral end of spermatophore. h, spermatophore.

TABLE 3
MEANS, STANDARD DEVIATIONS, AND RANGES OF SELECTED MEASUREMENTS AND INDICES (IN PER CENT) OF
Loliolus hardwickei (GRAY).

Measure/ Index	MALES				FEMALES			
	n	Mean	S.D.(n-1)	Range	n	Mean	S.D.(n-1)	Range
ML(mm)	10			22-52	10			35-69
MWI	10	34.0	5.6	29-46	10	35.2	8.4	27-53
HLI	10	22.0	2.9	18-27	10	24.6	7.1	16-41
HWI	10	36.1	2.9	33-42	10	35.3	3.4	30-41
EDI	10	16.7	1.1	15-19	8	14.7	1.2	13-17
FLI	10	67.5	3.7	59-71	10	68.1	1.8	64-70
FWI	10	79.8	3.7	74-85	10	81.2	6.1	72-90
FL/FW	10	84.0	7.0	72-94	10	85.0	5.0	76-95
FA(°)	10	106.2	8.6	96-124	10	103.0	6.4	94-114
AL _I I	9	23.0	1.7	19-25	10	22.2	1.8	20-26
AL _{II} I	10	40.4	3.2	36-45	10	36.6	3.4	31-43
AL _{III} I	9	52.2	5.5	48-62	10	48.5	4.5	40-58
AL _{IV} I	10	50.3	3.7	46-57	10	46.7	4.1	41-53
HAI	8	46.5	2.3	43-49				
TtLI	10	89.3	23.4	63-147	10	88.1	11.7	73-111
CtLI	10	28.8	5.9	22-38	10	29.3	2.8	25-34
AS _I I	10	0.89	0.09	0.8-1.0	10	0.73	0.08	0.6-0.8
AS _{II} I*	10	1.77	0.14	1.6-2.0	10	1.23	0.13	1.0-1.4
AS _{III} I*	10	2.03	0.16	1.9-2.3	10	1.52	0.18	1.3-2.0
AS _{IV} I	10	1.02	0.16	0.8-1.3	10	0.80	0.08	0.7-1.0
CISI	10	1.14	0.21	0.8-1.5	10	1.18	0.28	0.8-1.6
GWI	10	25.6	3.6	23-32	9	26.7	4.7	22-37
RLI	10	18.2	1.2	17-20	10	17.4	2.2	15-22
RWI	10	4.92	0.56	4.0-5.5	10	5.02	0.66	4.0-5.9
SpL(mm)	8	3.02	0.44	2.1-3.5				
SpL _I	8	6.57	0.56	6.1-7.7				
SpRI	8	76.1	3.1	71-79				
SpWI	8	3.38	0.61	2.8-4.8				

* suckers from dorsal row of A_{II} and A_{III} of males used.

ventral membrane slightly broader, extends to club tip, dorsal membrane terminates along proximal portion of dactylus. Aboral swimming keel arises about halfway along club, expands distally, terminates abruptly at tip. *Club sucker dentition* on carpal sucker rings with low, square tipped, well spaced teeth on distal margin, reduced on lateral margins and absent or barely discernable on proximal margin; largest suckers on manus with 20-29 very small, blunt triangular or truncate teeth on entire margin (Fig. 7f), lower proximally; proximal teeth not evident in all specimens; marginal anal suckers with 19-28 teeth similar to those of medial suckers, larger on lateral margins. Sucker rings of largest dactylus suckers with square tipped teeth on entire margin, teeth smaller and restricted to distal margins on distal suckers; proximal plates low; suckers at tip without dentition.

Buccal membrane with seven lappets, each bearing 1-6 minute suckers, ventral lappets generally with fewer suckers; each sucker bears 5-6 low semi-lunar teeth on the distal sucker ring margin, proximal plates smooth, low. Females with a large swollen seminal receptacle on the oral surface of the buccal membrane, between the ventral lappets. *Gladius* broad (GWI 22-37), vane very thin, fragile, widest at about half gladius length,

margins strongly curved posteriorly, anterior third of vane tapers sharply in a slightly concave curve to the free rachis; rachis very slender (RLI 15-22, RWI 4.0-5.9), weak, lateral supporting rods very weak, continue to posterior tip.

Upper beak with rostrum sharply pointed, slightly curved, width equal to length; rostral margin brown with dark brown to black tip, remaining area of rostrum and hood light brown. Hood length about 70% of crest length, wing length about 1.5 times the rostral length, cutting edge of wing irregularly serrated, a prominent tooth present at jaw angle. Crest curved, lateral wall large, only lightly pigmented anteriorly, posterior margin with deep indentation, margins of wing, hood, crest and lateral wall transparent. *Lower beak* with rostrum short, pointed, light yellowish brown except margins of rostrum which are dark brown, cutting edge of rostrum straight, irregularly serrated, rostral width approximately equal to rostral length. Hood short, about 1.5 times the rostral length, wing length about twice the rostral length, cutting edge of wing straight, irregularly serrated, a large tooth present at jaw angle. Hood light brownish, wing transparent. Crest curved, crest length about 2.5 times rostral length, lateral wall length about 3.5 times rostral length, very light brown

anteriorly, transparent posteriorly. *Radula* with seven transverse rows of teeth, rhachidian with a sharp slender median tooth, lateral cusps very low, rather blunt; first lateral tooth stout, sharp with a low sharp cusp; second lateral tooth straight, stout, tip slightly rounded; third lateral tooth slender, curved, sharp with a large basal plate; marginal plates very small, irregularly shaped.

Spermatophores (Fig. 7g,h) small (SLI 6.1-7.7), slender, sperm mass comprises 71-79% of total spermatophore length; cement body in two distinct parts, aboral part stout, oval shaped, connected to oral part by a slender neck; oral part short, stout, spirally sculptured, tapers abruptly to junction with the ejaculatory apparatus; middle tunic along cement body neck with one or two closely opposed angular ridges; ejaculatory apparatus tightly coiled, several coils in the slightly dilated oral extremity of the spermatophore.

Colour in isopropyl or ethyl alcohol cream or yellow-cream; body and dorsal surface of fins sparsely covered with large purplish chromatophores, smaller on ventral body surface, dorsal surface of fins with a concentration of small chromatophores at the fin margins, few chromatophores on main fin area, ventral fin surface lacking chromatophores. Dorsal surface of head and aboral surfaces of arms and tentacles with large, sparse chromatophores; dark semi-lunar patches dorsal to each eye; ventral surface of head and funnel without

chromatophores excepting a small patch in the funnel groove. No *photophores* present in this species. A pair of small papillae are located on the integument overlying the postero-ventral surface of the bulbous ink sac, anterior to renal openings, one on either side and slightly dorsal to intestine (Fig. 3c). The location of the papillae is similar to that of the photophores in *Loliolus noctiluca*. However, there is no structure beneath the papillae referable to photophores in *L. hardwickei*. These papillae are absent in females. The accessory nidamental glands are located in their place (Fig. 3d). The function of these papillae is unknown.

SIZE AT MATURITY: Males were observed to have spermatophores in the Needham's sac from about 30 mm ML, enlargement of the nidamental glands in females was not evident until 38-40 mm ML. The largest specimen observed was a female of 69 mm ML, from the Persian Gulf.

SYNTYPES: 1 male, 33 mm ML, 1 female, 49 mm ML, India, British Museum (Natural History), London, No. 1947. 3. 15. 1-2.

DISTRIBUTION: *Loliolus hardwickei* has a wide distribution, from the northern Persian Gulf, the Indian and Burmese coasts and throughout Indonesia (Fig. 8). A single specimen (ZMC) has been recorded from the Chinese coast, opposite Taiwan. This species is found in

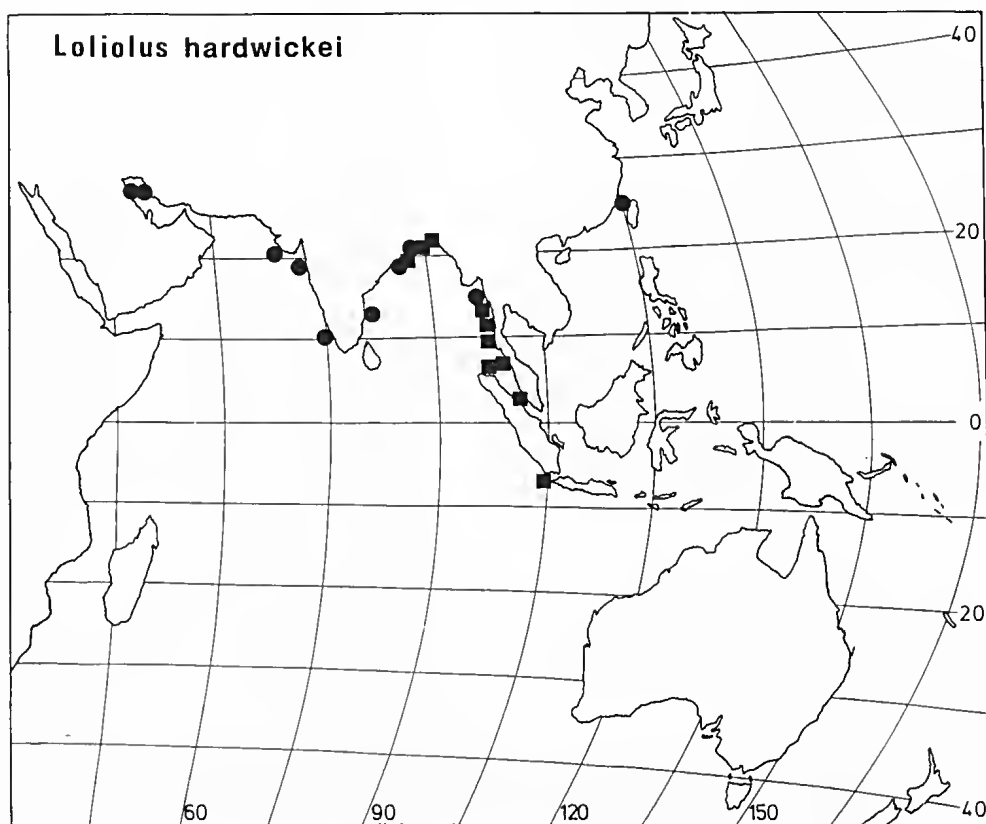


FIG. 8—Distribution records of *Loliolus hardwickei* (Gray). Solid squares represent literature records (see text). Solid dots represent new records. Gray's syntypes from India are not included.

estuaries and shallow coastal waters to a maximum recorded depth of 30 m.

REMARKS: *Loliolus typus* Steenstrup and *L. investigatoris* Goodrich are here synonymised with *L. hardwickei* (Gray), on the basis of a comparison of the type specimens of each. The syntypes of *L. hardwickei*, the holotype of *L. typus* and the syntypes of *L. investigatoris* are in a very good state of preservation and include males with a well developed hectocotylus. The species are considered conspecific primarily by a comparison of the hectocotylus of each, both bearing the proximal crest on the ventral membrane which is unique to this species. The material described as *L. typus* by Grimpe (1932) is referable to *L. affinis*; this is based on Grimpe's excellent illustration of the hectocotylus, matching exactly with that of *L. affinis*.

Massy (1916, p. 222) described a marked sexual dimorphism in this species, with males having longer arms and larger arm suckers. This is shown by the specimens examined but the difference is not so great as Massy appeared to believe. Adam (1939) noted no dimorphism, but in 1954 described the arm suckers of males as being larger in the ventral row. This does not appear to be so, although the ventral suckers may appear larger because of their smaller apertures in a similar sized cup as the dorsal row. Adam (1954) also noted the broader gladius in females. Adam (1954) considered that *Loliolus investigatoris* and *L. affinis* may be synonymous, but without detailing any reasons for this decision. Probably he was misled by Grimpe's (1932) erroneous identification and description of *L. affinis* as *L. typus*. He certainly noted the differences between Grimpe's material and his own.

Nesis (1982, p. 132) regarded *Loliolus investigatoris* Goodrich, 1896, *L. hardwickei* (Gray, 1849), and *L. rhomboidalis* Burgess, 1967, as valid species, and placed *L. typus* Steenstrup, 1856 and provisionally *L. affinis* Steenstrup, 1856 in synonymy with *L. hardwickei*. After examination of all type specimens, we conclude that *L. investigatoris*, *L. typus* and *L. hardwickei* are conspecific and that *L. affinis* is a distinct species. Nesis' provisional inclusion of *L. affinis* as a junior synonym of *L. hardwickei* was probably due to his acceptance of Grimpe's (1932) identification. This is evident by the fact that the figures shown as *L. hardwickei* by Nesis (Fig. 34d, e, e₁) are the figures of Grimpe's *L. typus* (Fig. 1B, 3A, 3B).

***Loliolus affinis* Steenstrup, 1856**

Figs 9, 10; Tables, 4, 5, 6

1856 *Loliolus affinis* Steenstrup, p. 194, pl. 1, fig. 6, 6'.

1932 *Loliolus typus*, Grimpe, p. 471-486, figs. 1-3.

1968 *Loliolus affinis*, Silas, p. 307.

1982 *Loliolus hardwickei*, Nesis, fig. 34 d, e, c₁.

MATERIALS EXAMINED: See APPENDIX 4.

DESCRIPTION: Animal small. *Mantle* slightly dorso-ventrally flattened; tapers very gradually posteriorly to a blunt rounded tip; median antero-dorsal lobe rounded, pronounced (Fig. 9a); ventro-lateral lobes pointed, con-

spicuous; ventral mantle margin between lobes deeply concave to accommodate funnel. *Fins* large, FLI=49-64, FWI=57-98; heart shaped, posterior margins straight, continuous around apex of mantle; anterior margins convex with slightly developed lobes; lateral lobes broadly rounded. Fin length and width indices increase with mantle length. The gladius is visible through the integument in the anterior two-thirds of the mantle, then submerges below the museles of the mantle and fins in the posterior one-third of the mantle. *Head* broad, short, as wide as mantle, dorso-ventrally flattened. Eyes large (EDI=14-29), a small pore present between the eye and base of third arm; olfactory apparatus conspicuous, with an indentation on posterior side of head. *Funnel* stout, bluntly tapered anteriorly, free in its anterior quarter; funnel and mantle locking cartilage simple, straight groove and ridge, strongly developed. Dorsal funnel organ large; lateral limbs very long, broad in posterior half, tapered to a rounded end posteriorly; anterior half of limb narrow with a swollen appearance. Apical papilla simple, thumb-like; ventral pads elongate, ovoid, both medial and lateral borders convexly curved, more so on lateral borders. Funnel valve very well developed, corners rounded, anterior border slightly convex.

Arms short, order III \geq IV, II, 1. Arm I laterally compressed with a distinct aboral keel for nearly its entire length. Arm II laterally compressed distally, a low aboral keel present along entire arm length. Arm III robust, laterally compressed with a very conspicuous, broad, aboral (swimming) keel that remains broad distally. Arm IV trapezoid in section, well developed tentacular sheath dorso-laterally, low angular keel ventro-medially. Protective membranes very broadly developed on all arms except on Arm IV where they are low and weak; trabeculae museular but do not extend beyond edge of protective membrane on Arms I-III; form scalloped border along membrane of Arm IV. Arm suckers larger in males. Suckers on ventral row of Arms II and III in males larger than those on dorsal row, suckers on Arm III largest, those on Arm I smallest. *Arm sucker dentition* shows chitinous rings of the largest suckers on Arm I with 3-4 truncate teeth on distal margin, proximal margin smooth or irregular. Dorsal row of suckers of Arms II and III in males and both dorsal and ventral rows of suckers in females with 3-7 low, rounded or trapezoidal teeth on distal and lateral margins, proximal plates very low, smooth (Fig. 9d); ventral suckers of Arms II and III of males with 3-5 large, higher trapezoidal teeth on distal and lateral margins, proximal margin smooth and higher than those on dorsal row (Fig. 9e), Arm IV with 3-6 low, truncate or trapezoidal teeth on distal margin, proximal margin smooth. Left ventral arm of males *hectocotylised* (Fig. 9b) generally equal to or shorter than right ventral arm (only 3 of 10 specimens examined have longer left ventral arm). Tentacular sheath very broad running along entire length of arm. Suckers and sucker stalks in ventral row entirely absent. Ventral protective membrane broad, thickened, becoming narrower toward arm tip;

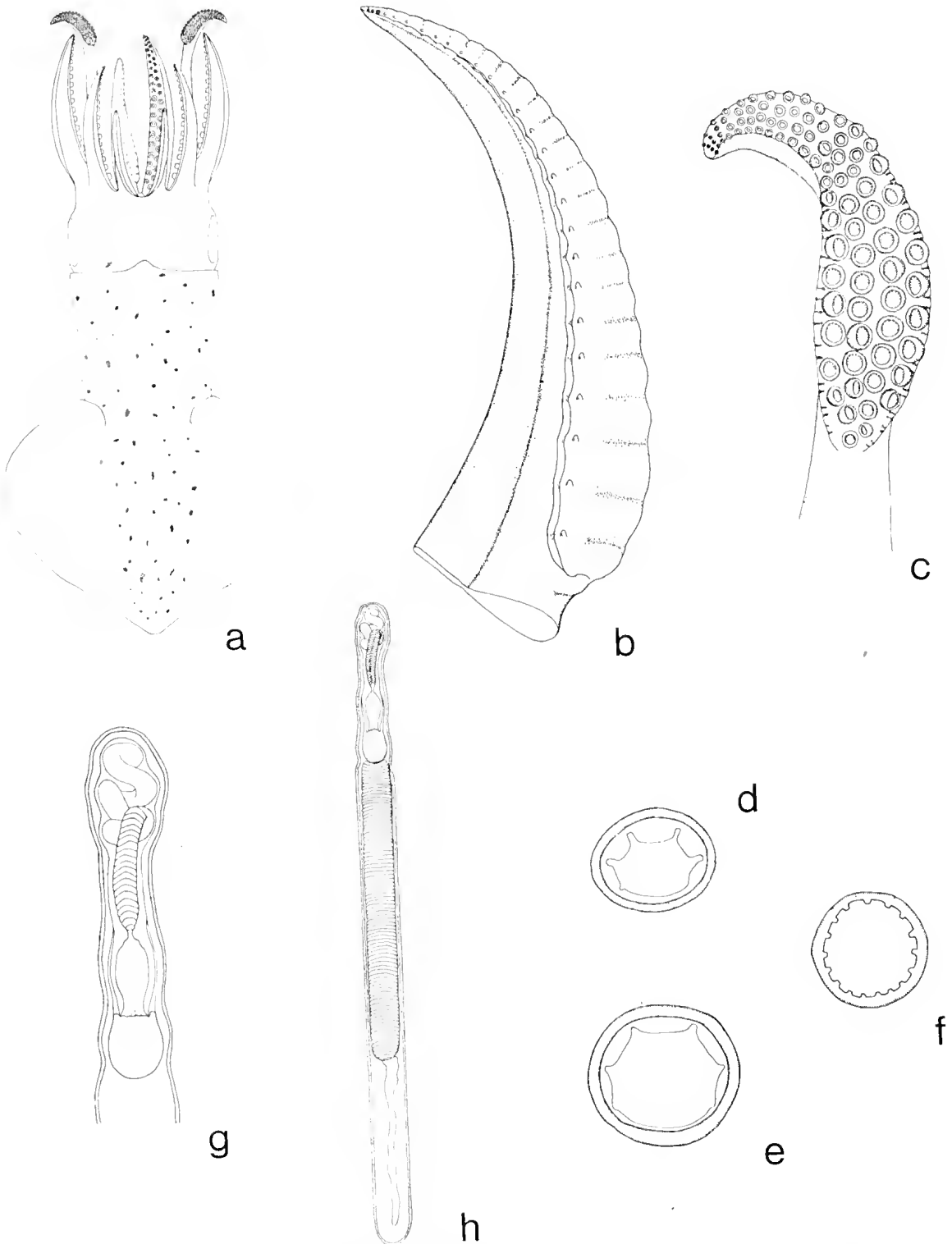


FIG. 9—*Loliolus affinis* Steenstrup. a, ZMC, male 24 mm ML, 12°10'N, 102°27'E, dorsal view. b, ZMC, 26 mm ML, 12°10'N, 102°27'E, hectocotylied arm. c, same specimen as (a), left tentacular club. d-e, CAS 030250, male 25 mm ML. d, largest sucker ring from dorsal row of third arm; e, sucker ring from the ventral row in same pair as (d) (d and e to same scale). f, same specimen as (a), largest club median manal sucker ring. g-h, same specimen as (a). g, oral end of spermatophore. h, spermatophore.

TABLE 4
MEANS, STANDARD DEVIATIONS, AND RANGES OF SELECTED MEASUREMENTS AND INDICES (IN PER CENT) OF
Lololus affinis STEENSTRUP.

Measure/ Index	MALES				FEMALES			
	n	Mean	S.D.(n-1)	Range	n	Mean	S.D.(n-1)	Range
ML(mm)	10			19-32	5			22-39
MWI	10	39.8	6.4	33-54	5	39.8	3.7	34-44
HLI	10	28.5	9.4	22-47	5	26.7	3.9	22-32
HWI	10	41.6	6.4	35-54	5	39.8	5.4	34-48
EDI	10	20.6	3.5	18-29	5	18.6	2.9	14-22
FLI	10	58.1	4.5	49-64	5	61.4	0.9	60-63
FWI	10	75.7	15.2	57-98	5	77.7	9.0	69-92
FL/FW	10	79.0	13.2	59-95	5	79.7	7.8	68-89
FA(°)	10	110.8	16.1	90-139	5	116.6	18.2	98-132
AL _I I	10	18.7	4.4	12-28	5	16.9	2.5	14-20
AL _{II} I	10	37.2	14.4	23-65	5	29.5	9.0	23-45
AL _{III} I	10	46.6	17.6	32-82	5	41.1	12.8	30-63
AL _{IV} I	9	41.2	13.3	27-69	5	38.5	9.7	32-56
HAI	7	40.9	10.7	33-63				
TtLI	7	59.6	26.8	54-87	5	104.0	58.1	58-200
CILI	7	19.3	2.5	15-23	5	23.9	4.5	20-29
AS _I I	7	0.76	0.22	0.5-1.0	4	0.62	0.07	0.5-0.7
AS _{II} I	7	1.33	0.54	0.9-2.2	3	0.88	0.08	0.8-0.9
AS _{III} I	7	1.48	0.67	1.0-2.5	3	1.12	0.14	1.0-1.2
AS _{IV} I	7	0.93	0.21	0.6-1.3	3	0.66	0.04	0.6-0.7
CISI	6	0.75	0.11	0.6-0.9	5	0.75	0.17	0.5-0.9
GWI	9	27.0	3.9	24-34	5	31.3	4.3	26-36
RLI	8	22.4	2.9	18-28	5	21.3	2.7	18-24
RWI	9	5.10	1.00	4.3-7.1	4	5.67	1.23	4.4-7.0
SpL(mm)	5			1.7-2.0				
SpLI	5	7.59	0.35	7.3-8.0				
SpRI	5	74.7	1.6	72-76				
SpWI	5	3.35	0.23	3.0-3.6				

trabeculae on ventral row greatly thickened, fused by the broad, fleshy, ventral protective membrane. Dorsal protective membrane thin, very narrow, diminishing distally, disappeared near arm tip. Trabeculae on dorsal row diminished, narrow, incorporated with the protective membrane producing a scalloped margin to the membrane. Suckers on dorsal row absent, diminutive papillae only remaining.

Tentacles relatively short, stalks naked and with small, slightly expanded clubs, CLI=15-29 (Fig. 9c). Club suckers tetraserial on manus and dactylus; carpal structures absent; manal suckers in 7-9 rows, larger and distinct from dactylus suckers; median suckers of manus slightly larger (1.1-1.3 times) than the diameter of marginal suckers. Dactyl suckers in approximately 15 tetraserial transverse rows, grading to minute distally; no distal circle of minute dactyl suckers exists. *Protective membranes* arise at the proximal end of the club, low. The protective membranes narrower along the dactylus; the ventral membrane extends to the tip of the dactylus, the dorsal membrane terminates along the proximal part of the dactylus. The swimming keel arises on the aboral angle of the club at about half its length. It expands very rapidly and becomes considerably broader than the oral surface of the dactylus, then terminates abruptly at the tip. *Club sucker dentition* (Fig. 9f) in-

cludes proximal-most suckers with chitinous rings that possess short truncate teeth around entire ring; largest distally, minute proximally. Rings of medial manal suckers with 15-20 small, truncate or blunt, well spaced teeth on entire margin, shorter proximally. The outer soft rings with minutely granular sculpture. Marginal manal sucker rings with 11-18 very small, blunt or truncate teeth, larger on lateral margins, reduced to minute protuberances medially. Dactyl sucker rings with numerous well-spaced, small, truncate to blunt teeth around entire margin.

Lappets of *buccal membrane* with 0-4 minute suckers each. Females bear a small buccal seminal receptacle on the convoluted oral surface of the buccal membrane between the ventral lappets. *Gladius* very broad (GWI 24-36), short, paddle shaped. Vane very thin, strongly curved posteriorly, widest in its anterior third; without thickenings. Free rachis short and wide (RLI 18-28, RWI 4.3-7.1), median groove rounded, shallow; lateral rods weak.

Upper beak with rostrum sharply pointed, long, curved; width equal to length; rostral margin brown with dark brown tip, remaining area of rostrum and hood light brown. Hood length about two-thirds crest length; wing length about twice rostral length, cutting edge of wing irregular, no notch or prominent tooth pre-

sent at jaw angle. Crest curved, lateral wall large, pigmented anteriorly, posterior margin with a deep indentation; posterior margins of wing, hood, crest and lateral wall transparent. *Lower beak* with rostrum short, pointed, light yellowish brown except margins of rostrum which are dark brown; cutting edge of rostrum straight, irregularly serrated, rostral width approximately equal to rostral length. Hood short, about twice rostral length, wing length about three times rostral length, cutting edge of wing straight, irregularly serrated; hood light brown with transparent margin. Wing transparent. Crest curved, crest length about four times rostral length; lateral wall length about five times rostral length, light brown at centre, transparent around margins. *Radula* with seven transverse rows of teeth, rhachidian slender, sharp with low, sharp lateral cusps; first lateral tooth small, sharp, cusp very low, pointed; second lateral tooth straight or slightly curved, sharp, no cusps; third lateral tooth curved, slender, sharp; marginal plates small, approximately equal in length and width.

Spermatophores (Fig. 9g,h) small SLI 7.3-8.0, sperm mass comprises 72-76% of total length; cement body in two distinct parts, aboral part stout, ovoid, connected

to oral part by a slender neck; oral part moderately long, dilated, tapers gradually to junction with the ejaculatory apparatus; middle tunic does not follow contour of the cement body; slight spiral sculpturing along oral end of cement body; ejaculatory apparatus strongly coiled, several coils in the slight dilation at the oral extremity of the spermatophore.

Colour in isopropyl alcohol cream, with brown to dark maroon chromatophores distributed evenly over mantle, head and aboral surface of arms; chromatophores on dorsal surface of mantle and head usually larger and more concentrated than on ventral surface. A broad band of large chromatophores extend along dorsal midline of fins. The ventral surfaces of fins are devoid of chromatophores. No *photophore* is present. Males possess one pair of small papillae on the ink sac, identical to that described for *L. hardwickei*.

SIZE AT MATURITY: Spermatophores are present in males as small as 22 mm ML. The nidamental glands of females began enlargement at a similar size, but no mature female was found in the material studied. The largest male specimen studied is 32 mm ML and the largest female examined is 39 mm ML.

TABLE 5
MEASUREMENTS OF HOLOTYPES AND SYNTYPES OF ALL SPECIES OF *Loliolus* STEENSTRUP 1856.
(Except where otherwise indicated, all measurements are in millimetres.)

	<i>L. hardwickei</i> Syntype	<i>L. hardwickei</i> Syntype	<i>L. typus</i> Holotype	<i>L. affinis</i> Syntype	<i>L. affinis</i> Syntype	<i>L. investigatoris</i> Syntype	<i>L. investigatoris</i> Syntype	<i>L. investigatoris</i> Syntype	<i>L. noctiluca</i> Holotype
Sex	♂	♀	♀	♂	♀	♂	♀	♀	♂
ML	33	49	27	32	39	22	33	35	59
VML	32	40	23	32	38	19	31	31	54
MW	14	17	13	15	16	10	13	13	17
HL	11	14	9	10	9	5	9	9	11
HW	13	13	14	14	13	9	13	13	17
ED	6	7	7	8	7	4	5	6	8
FL	23	32	17	20	24	13	23	24	36
FW	29	43	22	32	31	17	27	25	43
FA(°)	134	104	127	118	112	124	101	102	108
AL _I	9	12	6	7	7	4	8	7	14
AL _{II}	20	21	17	12	9	8	15	13	20
AL _{III}	23	27	23	18	16	14	20	18	23
AL _{IV}	18	24	16	14	14	12	17	17	22
HcA1	18		16	14		12	15		22
TiL	55	66	44		44	33	29	30	38
CiL	10	21	7		8	8	8	9	18
AS _I	0.4	0.3	0.2			0.2	0.3	0.2	0.4
AS _{II} *	0.7	0.5				0.3	0.6	0.4	0.5
AS _{III} *	0.7	0.6				0.4	0.7	0.5	0.6
AS _{IV}	0.4	0.4	0.3			0.2	0.4	0.2	0.3
CIS	0.3	0.7	0.3		0.2	0.2	0.3	0.3	1.6
SpL							2.1		5.0
NL		10			8.4			6.5	
GW			9		13	7	11	9	13
RL			6.6		7.7	4.5	6.4	6.7	9.4
RW			1.7		2.5	1.2	1.8	2.0	2.3

* suckers from dorsal row of AL_{II} and AL_{III} of males used.

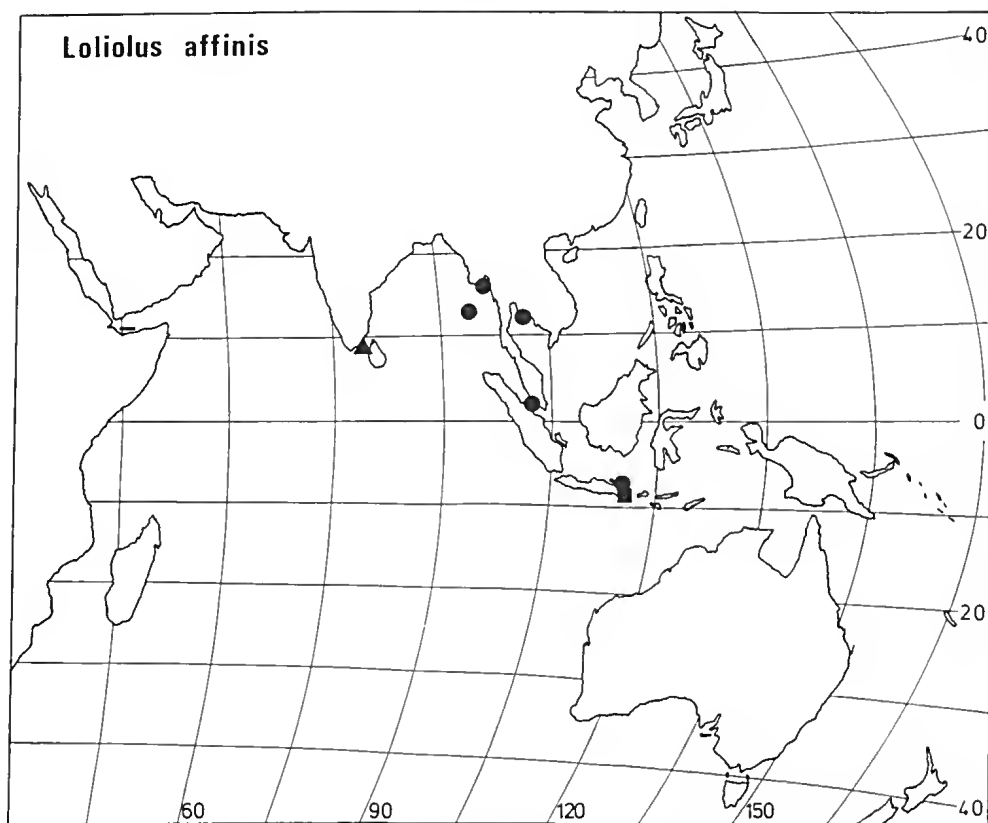


FIG. 10—Distribution records of *Loliolus affinis* Steenstrup. Solid triangle—type locality (approximate). Solid squares—literature records (see text). Solid dots—new records.

SYNTYPES: 1 male, 32 mm ML, 1 female, 39 mm ML, Zoological Museum, University of Copenhagen.

TYPE LOCALITY: "Captured by Governor Christensen on a voyage from the Cape [C. Comorin?] to Tranquebar [India]" (Steenstrup 1857, p. 89). Specimens probably then come from the Gulf of Manaar, Palk Strait region, southern India.

DISTRIBUTION: *Loliolus affinis* is widely distributed in the Bay of Bengal and southeast Asian waters. It has been recorded from southern India (type) and East Java (Grimpe 1932). New records for this species are from the eastern Bay of Bengal, Andaman Islands, southern Malaya, and the Gulf of Thailand (Fig. 10).

SUBMERGENCE OF *Loliolus steenstrupi* AND *Loliolus rhomboidalis*

Loliolus steenstrupi Dall, 1871, based on a single specimen from the Gulf of California, was very inadequately described without illustration or designated type specimen, and Berry (1929, p. 278) claimed it should be "thrown into limbo as unidentifiable". Berry recognized that his *Loliopsis chiroctes* Berry, 1929 possibly could be Dall's *steenstrupi*. This may be so, but Dall's description and the absence of any specimens does not permit it to be placed in synonymy. Thorough searching at NMNH

confirms that no type exists, and indeed, it must be considered a *nomen dubium*.

Loliolus rhomboidalis was described by Burgess (1967) based on specimens collected from the Bay of Bengal and the Andaman Sea. The species is sufficiently different from other congeners that Burgess redefined the genus to accommodate her new species. Natsukari (1983) reported that the original description and illustrations of *Loliolus rhomboidalis* apply very well to *Loligo kubiensis* Hoyle, 1885. Thus, he placed *Loliolus rhomboidalis* in synonymy with *Loligo kubiensis*. During the present study, additional material of *L. rhomboidalis* from the eastern Gulf of Thailand, as well as the holotypes of *Loligo kubiensis* and *Loliolus rhomboidalis* were examined. We agree with Natsukari's conclusion that *rhomboidalis*, being the only species to possess several normal suckers on the proximal portion of the hectocotylised arm and the only species to have rhomboidal fins, does not belong to the genus *Loliolus*. We accept Natsukari's decision to place *Loliolus rhomboidalis* in synonymy with *Loligo kubiensis*.

COMPARISON OF SPECIES

The genus *Loliolus* was erected by Steenstrup (1856), who separated it from the genera *Loligo* and *Sepioteuthis* on the basis of the hectocotylised arm

which "throughout its whole length it has not the least trace of a sucker, the surface on which the suckers should be situated being even converted into a compressed, obtusely-toothed edge; we find that all the teeth of this edge are produced from the fused bases of the peduncles of the inner series of acetabula, whilst those of the other row scarcely the smallest trace is left" (Steenstrup 1857, p. 89). Burgess (1967) redefined the genus as having up to seven normal suckers on the proximal portion of the hectocotyliised arm. Following the conclusion reached by Natsukari (1983) and us to synonymise *L. rhomboidalis*, the original definition of the genus as defined by Steenstrup should be retained. The genus *Loliolus* is thus defined as a loliginid squid with heart-shaped fins, with the whole length of the left ventral arm of the male hectocotyliised and with no normal suckers on the proximal portion of the hectocotyliised arm. Of the six nominal species previously placed in the genus *Loliolus*, i.e., *L. hardwickei*, *L. typus*, *L. affinis*, *L. investigatoris*, *L. steenstrupi*, and *L. rhomboidalis*, only *L. hardwickei* and *L. affinis* are recognised as valid. The genus now contains *L. hardwickei* (Gray), *L. affinis* Steenstrup, and *L. noctiluca* n. sp.

Loliolus noctiluca may be readily distinguished from other *Loliolus* by the presence of a pair of luminescent organs, a conspicuously papillated hectocotylus, and large, smooth ringed manal suckers. Each of these features is unique within the genus. The presence of luminescent organs on *L. noctiluca* is of interest. Examination of *L. hardwickei* and *L. affinis* reveals that comparable luminescent organs are lacking in these species. In the males of these species, a pair of papillae with a small orifice is located on the ink sac, anterior to the renal opening, similar to the location of luminescent organs in *L. noctiluca*. However, unlike *L. noctiluca* where the orifice opens into the bean-shaped organ, in the males of other congeners there is no structure beneath this orifice that is referable to a luminescent organ. These papillae with orifice are absent in the females of both species. The accessory nidamental glands are located in the position of the papillae. The function of these papillae is unknown.

The other members of the genus may be distinguished from each other by comparison of the hectocotyliised arms: *L. hardwickei* bears a large proximal crest which is absent in *L. affinis*. Both *L. hardwickei* and *L. affinis* bear modified suckers on Arms II and III of the males. In *L. hardwickei* the suckers on the dorsal row are larger while the reverse is true in *L. affinis*. The tentacular club of *L. hardwickei* and *L. affinis* are similar, being barely expanded and with median and marginal manal suckers of subequal size. The clubs of *L. noctiluca* are greatly expanded and exhibit a large disparity in size between median and marginal manal suckers. A detail comparison of characters separating species of the genus *Loliolus* is found in Table 6.

KEY TO THE SPECIES OF *LOLIOLUS*

1. One pair of luminescent organs present on ink sac,

- rings of large manal suckers smooth, hectocotylus conspicuously papillated *L. noctiluca*
- No luminescent organs on ink sac, large manal sucker rings not smooth, hectocotylus not conspicuously papillated 2
- 2. Hectocotyliised arm with a large proximal crest *L. hardwickei*
- No proximal crest present on hectocotyliised arm *L. affinis*

DISCUSSION

The genus *Loliolus*, the third earliest loliginid genus to be erected, appears to be a natural, well-defined group readily distinguishable from other genera in the family Loliginidae. Members of the genus *Loliolus* differ from other loliginid genera in having heart-shaped fins and in having the whole length of the left ventral arm in males hectocotyliised with no normal suckers on the proximal portion of the arm. The fins of other loliginid are rhomboidal except in *Sepioteuthis* which has lateral fins similar to those in *Sepia*. The hectocotylus of all other loliginids affects only the distal portion of the arm with normal suckers retained on the proximal portion of the arm.

Luminescent organs have been described for a number of Indo-West Pacific loliginid squid: *Loligo edulis* (Okada, 1927), *L. chinensis* (Okada, 1927), *Doryteuthis sibogae* (Natsukari, 1976) and *Uroteuthis bartschii* (Haneda, 1963). Luminescent organs have not been reported from loliginids of the eastern Pacific and Atlantic Oceans.

Okada (1927) described the light organs of *L. edulis* as a pair of flat organs on each side of the ink sac and stated that they were the same as those of the Sepiolidae both externally and internally. Kishitani (*vide* Haneda 1963) cultivated luminescent bacteria from the ink sac organs of *L. edulis*. A detailed account of observations in living specimens, structure of the light organ, and the culture of luminescent bacteria in *U. bartschii* was presented by Haneda (1963).

The light organs described for *L. noctiluca* appear similar to those described for *Loligo* and *Uroteuthis*, both externally and in gross anatomy. Thus, the light organs in *L. noctiluca* are most likely functioned by symbiotic luminous bacteria, although no luminous activity has been observed. The absence of a functional light organ and, in males, the presence of a papilla in its place in *L. hardwickei* and *L. affinis* are of interest. The fact that light organs do not occur in all members of *Loliolus* is comparable to that in the genus *Loligo* where not all members possess light organs. The presence of one pair of papillae in the males and their absence in the females of two members of *Loliolus* is without parallel in Loliginidae. In a thorough examination of material on hand, which includes specimens of *Loligo japonica*, *L. pealei*, *L. vulgaris*, *Loliguncula brevis*, *Alloteuthis media*, *A. subulata* and *Doryteuthis plei*, no similar papillae were found.

Boletzky (1971) described a pair of organs of

TABLE 6
COMPARISON OF SELECTED CHARACTERS OF THE THREE SPECIES OF *Loliolus*.

Species	Type Specimens	Size at Maturity and Maximum Size Known	Luminescent Organs	Arm Suckers, A _{III}
<i>L. hardwickei</i> (Gray)	<i>hardwickei</i> : Syntypes, male, 33 mm ML, female, 49 mm ML, India (BMNH)			
= <i>L. typus</i> Steenstrup	<i>typus</i> : Holotype, male, 27 mm ML, locality unknown (ZMC)	Mature: males: 30 mm ML females: 38-40 mm ML	Absent	Suckers of dorsal and ventral rows in males sub- equal in size but those on ventral row with smaller aperture
= <i>L. investigatoris</i> Goodrich	<i>investigatoris</i> : Syntypes, 2 males, 22-33 mm ML; 4 females, 35-47 mm ML, Bay of Bengal (ZMC)	Max. Size: males: 53 mm ML females: 69 mm ML		
<i>L. affinis</i> Steenstrup	Syntypes, male, 32 mm ML; female, 39 mm ML, S.E. Indian Coast (ZMC)	Mature: males: approx. 22 mm ML females: no mature specimen was found Max. Size: males: 32 mm ML females: 39 mm ML	Absent	Suckers on ventral row in males larger than those on dorsal row
<i>L. noctiluca</i> n.sp.	Holotype, male, 59 mm ML, Northern Port Phillip Bay, Victoria Australia (NMV)	Mature: both sexes: 40-50 mm ML Max. Size: males: 62 mm ML females: 83 mm ML	One pair on ink sac	Suckers on dorsal and ventral rows in both sexes similar

unknown function which he called "epirenal bodies" in male *Neorossia caroli*. The position and the superficial appearance of these organs are similar to the above-mentioned papillae in *Loliolus*. We suspect these papillae in the males of *L. hardwickei* and *L. affinis* probably represent vestiges of retrogressive light organs, and in the females, these organs have totally degenerated. However, as stated by Boletzky (1971) on *Neorossia caroli*, the entire complex comprising the papillae, the accessory nidamental glands, and the light organs need to be investigated in order to determine the true nature of these papillae. A detailed study of the light organs in *Loliolus*, whether functional or rudimentary, must wait until adequate material becomes available. Such a study on *L. noctiluca* is being planned.

The location on the body of a female loliginid squid where spermatophores are affixed during copulation is generally considered to be of taxonomic value. Steenstrup (1881, p. 242), on the genus *Lolliguncula* and its type species, *L. brevis*, pointed out the fact that the females received spermatophores on the inner wall of the mantle, near the left gills. In 1887 (Volsøe *et al.* 1962, p. 203) Steenstrup re-affirmed the "difference in the mode of placing of the spermatophores" between

Loligo and *Lolliguncula*. For the genus *Loligo*, Steenstrup (1856, p. 110) reported that the spermatophores were attached to the lips (i.e., buccal membrane) of the female. Steenstrup's statement on the difference of the mode of attachment of spermatophores between *Loligo* and *Lolliguncula* was followed by Naef (1912, pp. 743-744). This seemingly clear-cut difference was later found to be over-simplified. Drew (1911, pp. 327-328) reported that in *Loligo pealei*, spermatophores were found to be attached either on the seminal receptacle, located on the buccal membrane, or on the left side of the inner mantle wall. McGowan (1954) and Fields (1965) reported a similar situation in *Loligo opalescens*. Attachment of spermatophores on the inner mantle wall of the females is, therefore, not restricted to the members of *Lolliguncula*. Examination of material on hand of *Lolliguncula* confirms the absence of a buccal seminal receptacle on *L. brevis* and the spermatophores are attached on the inner mantle wall near the left gill. On the other hand, in all three gravid female specimens of *L. mercatoris*, a buccal seminal receptacle, a structure that has not been described to date, is clearly present. The presence of the seminal receptacle on the buccal membrane of the females of all three species of

Arm Sucker Dentition, A _{III}	Club	Club Manal Suckers	Dentition of Largest Manal Suckers	Hectocotylus
Dorsal row in males and both dorsal and ventral rows in females with 3-7 low square teeth distally; ventral row in males with 2-4 large, trapezoidal teeth distally	Small, CILI = 22-38%, slightly expanded	Small, CISI = 0.8-1.6%, medial suckers 1.0-1.3 times the size of marginal suckers	20-29 small, well spaced truncate or rounded teeth on entire margin	Ventral protective membrane enlarged, thickened, fleshy, raised into tall crest proximally. Dorsal suckers reduced to minute papillae, dorsal protective membrane normal
Dorsal row in males and both dorsal and ventral rows in females with 3-7 low, rounded or trapezoidal teeth on distal and lateral margin, ventral row in males with 3-5 large, trapezoidal teeth distally	Small, CILI = 15-29%, slightly expanded	Small, CISI = 0.5-0.9%, medial suckers 1.1-1.3 times the size of marginal suckers	15-20 small, truncate or blunt, well spaced teeth on entire margin	Ventral protective membrane enlarged, thick, fleshy, no proximal crest. Dorsal suckers reduced to minute papillae, dorsal protective membrane thin, narrow, diminishes distally
4-7 large, truncate or round teeth in distal half, proximal margin smooth	Large, CILI = 25-41%, greatly expanded	Large, CISI = 1.7-3.4%, medial suckers 3-6 times the size of marginal suckers	Smooth	Dorsal and ventral rows with enlarged papillae, larger ventrally. Ventral papillae only partially fused to ventral protective membrane

Loliolus and the discovery of the "spermatophore pad" on the left funnel adductor muscle of some individuals of *L. noctiluca* again demonstrates the need for a critical investigation to delineate the genera in the family Loliginidae.

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APPENDIX 1
MATERIALS EXAMINED: *Loliolus noctiluca*

Sex	ML (mm)	Reg. No.	Location		Date	Depth (m)	Collector
Holotype							
M	59	NMV F31119	37°53'S,	144°56'E	29-x-80	9	FRV "Sarda"
Paratypes							
M	53	USNM 813977	37°51'S,	144°56'E	10-ii-76	6	CFE Roper
M	60	NMV F31120	37°53'S,	144°56'E	29-x-80	9	FRV "Sarda"
M	58	NMV F31121	37°53'S,	144°56'E	29-x-80	9	FRV "Sarda"
M	62	NMV F31122	37°53'S,	144°56'E	29-x-80	9	FRV "Sarda"
M	52	USNM 813798	37°53'S,	144°56'E	29-x-80	9	FRV "Sarda"
F	33	NMV F31123	38°21'S,	145°13'E	9-iv-75	—	M.U.Z.D.
F	58	NMV F31124	27°15'S,	153°15'E	26-iii-81	—	"Rejoice"
F	56	USNM 813799	27°15'S,	153°15'E	26-iii-81	—	"Rejoice"
M	52	QM M010577	27°15'S,	153°15'E	26-iii-81	—	"Rejoice"
F	58	QM M010578	27°15'S,	153°15'E	26-iii-81	—	"Rejoice"
M	54	AM C129497	08°45'S,	146°25'E	7-vi-61	—	DAS Fisheries
F	61	AM C129497	08°45'S,	146°25'E	7-vi-61	—	DAS Fisheries

APPENDIX 2
OTHER MATERIAL OF *Loliolus noctiluca* EXAMINED

No.	Sex	ML (mm)	Reg. No.	Location		Date	Depth (m)	Collector
1	M	55	NMV F31191	38°21'S,	145°13'E	3-ix-1974	—	M.U.Z.D.
1	M	52	NMV F31190	38°21'S,	145°13'E	8-vi-1974	—	M.U.Z.D.
1	M	49	NMV F31204	38°21'S,	145°13'E	7-vi-1974	—	M.U.Z.D.
1	F	55	NMV F31204	38°21'S,	145°13'E	7-vi-1974	—	M.U.Z.D.
1	M	35	NMV F31203	38°21'S,	145°13'E	9-iv-1975	—	M.U.Z.D.
2	F	35-38	NMV F31203	38°21'S,	145°13'E	9-iv-1975	—	M.U.Z.D.
1	F	59	NMV F31192	38°36'S,	146°55'E	21-vii-1979	—	J. Beumer
13	M	42-62	NMV F31130	37°53'S,	144°56'E	29-x-1980	9	FRV "Sarda"
2	F	38-60	NMV F31130	37°53'S,	144°56'E	29-x-1980	9	FRV "Sarda"
1	F	83	AM C126821	34°00'S,	151°13'E	14-x-1974	5	V. Wadley
1	M	44	NMV F31205	Gippsland Lakes, Victoria		—	—	B. Rigby
1	F	35	NMV F31208	38°37'S,	145°32'E	17-i-1980	46	"Mary Kain"
1	M	50	NMV F31194	Gippsland Lakes, Victoria		—	—	J. Beumer
2	F	41-54	NMV F31199	38°36'S,	146°55'E	11-xii-1979	—	J. Beumer
1	M	46	NMV F31197	Gippsland Lakes, Victoria		—	—	J. Beumer
1	M	43	NMV F31198	38°21'S,	145°13'E	9-iv-1975	—	M.U.Z.D.
1	F	33	NMV F31198	38°21'S,	145°13'E	9-iv-1975	—	M.U.Z.D.
1	M	50	NMV F31209	38°36'S,	146°55'E	21-vii-1979	—	J. Beumer
1	F	47	NMV F31195	38°36'S,	146°55'E	13-xii-1979	—	J. Beumer
1	F	65	NMV F31202	38°36'S,	146°55'E	13-xii-1979	—	J. Beumer
1	F	61	NMV F31206	37°52'S,	148°02'E	10-viii-1979	—	J. Beumer
1	M	61	NMV F31625	37°53'S,	147°49'E	6-viii-1979	3-5	D. Hobday
1	F	59	NMV F31625	37°53'S,	147°49'E	6-viii-1979	3-5	D. Hobday
1	F	75	NMV F31627	37°59'S,	147°44'E	5-viii-1979	3-5	D. Hobday
2	M	32-43	NMV F31630	Lake Victoria, Victoria		4-viii-1981	3-5	D. Hobday
1	F	27	NMV F31630	Lake Victoria, Victoria		4-viii-1981	3-5	D. Hobday
5	M	21-53	NMV F31200	37°53'S,	144°56'E	29-x-1980	10	FRV "Sarda"
1	M	54	NMV F31201	38°05'S,	145°07'E	—	—	G. Carruthers
1	F	42	NMV F31201	38°05'S,	145°07'E	—	—	G. Carruthers
2	M	60-60	NMV F31632	27°40'S,	153°29'E	6-xi-1981	32	"Iron Summer"
1	F	69	NMV F31632	27°40'S,	153°29'E	6-xi-1981	32	"Iron Summer"
4	M	43-48	NMV F31207	Moreton Bay, Qld.		26-iii-1981	—	"Rejoice"
4	F	36-55	NMV F31207	Moreton Bay, Qld.		26-iii-1981	—	"Rejoice"
42	M	20-60	NMV F31211	37°53'S,	144°56'E	29-x-1980	9	FRV "Sarda"
4	F	37-62	NMV F31211	37°53'S,	144°56'E	29-x-1980	9	FRV "Sarda"

APPENDIX 2 *continued*
OTHER MATERIAL OF *Lololus noctiluca* EXAMINED

No.	Sex	ML (mm)	Reg. No.	Location	Date	Depth (m)	Collector
3	F	52-65	NMV F31193	Botany Bay, NSW	3-ii-1981	—	G. Cuthbert
1	M	44	NMV F31196	Moreton Bay, Qld.	27-ii-1981	11-16	M. Potter
5	F	52-70	NMV F31196	Moreton Bay, Qld.	27-ii-1981	11-16	M. Potter
4	M	49-56	NMV F31210	16°43'S, 145°40'E	7-v-1981	6	"Southern Ocean"
6	F	44-70	NMV F31210	16°43'S, 145°40'E	7-v-1981	6	"Southern Ocean"
1	M	23	NMV F31629	27°36'S, 153°19'E	—	—	V. Wadley
1	M	15	NMV F31681	Moreton Bay, Qld.	—	—	CSIRO
3	F	49-73	NMV F31626	Moreton Bay, Qld.	22-vii-1981	—	"Alwayne"
2	M	39-39	NMV F31634	42°55'S, 147°35'E	----1979	—	S. Bell
2	F	45-52	NMV F31634	42°55'S, 147°35'E	----1979	—	S. Bell
5	M	26-36	NMV F31637	Storm Bay, Tas.	27-iv-1977	—	"Panghana"
6	F	28-39	NMV F31637	Storm Bay, Tas.	27-iv-1977	—	"Panghana"
5	M	33-42	NMV F31635	42°56'S, 147°25'E	23-vi-1976	—	Tas. Fish. Dev. Auth.
1	M	33	NMV F31633	33°49'S, 152°17'E	9-ix-1981	9-15	FRV "Kapala"
1	F	66	NMV F31636	37°53'S, 147°52'E	--vi-1979	—	Vic. Fish.
1	M	61	NMV F31638	37°52'S, 144°56'E	----1876	—	D. Kershaw
2	F	35-54	NMV F31639	37°51'S, 144°54'E	2-ii-1947	—	H. Morrison
2	F	41-47	NMV F31640	37°52'S, 144°56'E	--xii-1878	—	—
1	F	74	NMV F31641	Gippsland Lakes, Vic.	----1939	—	T. Yates
1	F	42	NMV F31642	Locality unknown	—	—	—
1	F	43	NMV F31643	37°55'S, 144°59'E	--v-1878	—	—
1	F	39	NMV F31644	37°55'S, 144°59'E	--vii-1866	—	—
1	M	48	NMV F31645	Sandridge, Vic.?	--xii-1872	—	—
1	F	61	NMV F31645	Sandridge, Vic.?	--xii, 1872	—	—
1	M	34	NMV F31646	Locality unknown	—	—	—
1	M	45	AM C102666	33°51'S, 151°10'E	16-iii-1972	8	H. Reeher & J. Paxton
1	F	48	AM C102666	33°51'S, 151°10'E	16-iii-1972	8	H. Reeher & J. Paxton
1	M	42	AM C126820	Sydney Fish Market	--v-1977	—	—
3	M	39-44	AM C102661	34°00'S, 151°13'E	18-iii-1975	3	V. Wadley
2	F	59-72	AM C102662	34°00'S, 151°13'E	21-xi-1974	5	V. Wadley
2	M	33-54	AM C131855	34°00'S, 151°14'E	26-8-i-1971	—	NSW Fish.
2	F	42-43	AM C131855	34°00'S, 151°14'E	26-8-i-1971	—	NSW Fish.
2	F	55-61	AM C36839	Port Jackson, NSW	—	—	—
1	M	42	AM C131851	Lake Macquarie, NSW	----1953	—	—
1	F	52	AM C131851	Lake Macquarie, NSW	----1953	—	—
1	F	61	AM C56308	23°52'S, 151°20'E	--vi-1930	—	W. Bedsor
1	M	41	AM C126818	23°52'S, 151°12'E	--iii-1977	—	P. Saenger
2	F	50-52	AM C131852	17°24'S, 140°07'E	1963-1964	—	CSIRO
3	M	31-55	AM C126829	17°24'S, 140°08'E	--xii-1976	7	CSIRO
3	F	35-45	AM C126829	17°24'S, 140°08'E	--xii-1976	7	CSIRO
1	F	50	AM C131850	17°24'S, 140°46'E	--xii-1963	—	CSIRO
4	M	48-52	AM C131846	16°23'S, 141°10'E	20-vi-1964	4.5	CSIRO
3	F	47-62	AM C131846	16°23'S, 141°10'E	20-vi-1964	4.5	CSIRO
1	F	41	AM C126825	17°25'S, 140°43'E	--xii-1976	3.5	CSIRO
1	F	45	AM C119565	8°47'S, 146°33'E	7-vi-1961	—	DAS Fisheries
1	M	50	AM C127910	7°57'S, 145°46'E	4-iv-1955	—	DAS Fisheries
3	F	56-64	AM C127910	7°57'S, 145°46'E	4-iv-1955	—	DAS Fisheries
1	M	45	AM C127905	8°51'S, 146°36'E	22-v-1969	—	DAS Fisheries
15	M	25-54	USNM 813974	37°51'S, 144°56'E	10-ii-1976	6	CFE Roper
14	F	14-68	USNM 813974	37°51'S, 144°56'E	10-ii-1976	6	CFE Roper

APPENDIX 3
MATERIALS EXAMINED: *Loliolus hardwickei*

No.	Sex	ML (mm)	Source & Reg. No.	Location	Date	Depth (m)	Collector
<i>Syntypes</i>							
1	♂	33	BMNH	India	1836	—	General Hard- wicke
1	♂	49	1947.3.15.1-2	India			
<i>Other material</i>							
1	♂	27†	Z.M.C.	Unknown	—	—	—
1	♂	22*	IM 44A = $\frac{3645}{7}$	21°39'N, 88°39'E	—	—	HMS "Investigator"
1	♂	33**	IM 45A = $\frac{3646}{7}$	21°39'N, 88°39'E	—	—	HMS "Investigator"
1	♀	35*	IM 47A = $\frac{7783}{6}$	15°13'N, 97°47'E	—	—	HMS "Investigator"?
1	♀	39	IM $\frac{423}{1}$	19°23'N, 85°09'E	—	14-17	HMS "Investigator"?
1	♀	45	IM $\frac{424}{1}$	13°05'N, 80°20'E	—	—	HMS "Investigator"?
1	♀	47	IM $\frac{425}{1}$	13°05'N, 80°20'E	—	—	HMS "Investigator"?
4	♂	35-40	Z.M.C.	29°57'N, 49°08'E	4-III-1938	10	G. Thorson
2	♀	56-65					
4	♂	45-52	Z.M.C.	29°18'N, 50°27'E	4-III-1937	20-24	G. Thorson
4	♀	49-69					
1	♂	40	CAS 030251	11°17'N, 75°47'E	13-I-1941	—	A.W.C. Herre
6	♂	27-35	UMML 1789	21°23'N, 69°46'E	16-XI-1963	18	R.V. 'Anton Bruun'
2	♀	38-40		21°24'N, 69°44'E			
1	♀	38	Z.M.C.	25°11'N, 119°28'E	10-IV-1897		Schönau
2	♀	36-38	Z.M.C.	18°48'N, 72°37'E	12-V-1964	20-30	Jørgen Nielsen

† Holotype of *L. typus* Steenstrup 1856.* Syntypes of *L. investigatoris* Goodrich, 1896.** Illustrated syntype of *L. investigatoris*.

APPENDIX 4
MATERIALS EXAMINED: *Loliolus affinis*

No.	Sex	ML (mm)	Source & Reg. No.	Location	Date	Collector
<i>Syntypes</i>						
1	♂	32	Z.M.C.	Gulf of Manaar		Gov.
1	♀	39		Palk Strait Region, India		Christensen
<i>Other material</i>						
4	♂	19-26	Z.M.C.	12°10'N, 102°27'E	30-XII-1899	Th.
1	♀	29		Coast of Ban Lem Ngop (Thailand)		Mortensen
2	♂	21-25	CAS 030250	Andaman Islands	1940	Herre Expedition
1	♀	27	Z.M.C.	16 km from Rangoon Hbr, Burma	18-XI-1863	Hansiu and Thalbitzen
1	♀	22	Z.M.C.	South Malacca		Poul Fogh
22	♂	10-27	Z.M.C.	Surabaya	1870	Andrea
9	♀	10-26				

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A NEW LUNGFISH FROM THE LOWER CARBONIFEROUS OF VICTORIA, AUSTRALIA

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ABSTRACT: *Delatitia* gen. nov. (type species *Ctenodus breviceps* Woodward), is described from a skull roof and isolated toothplates from the Lower Carboniferous Mansfield Group, Victoria. The new genus is similar to *Ctenodus* in the arrangement of bones B, C, D, I, J and L, but differs in having long E bones, a narrow Y1, Z not completely enclosed laterally by Y2, and the occipital sensory-line running posteromesially out of the I bones. Its toothplates have flat radiating tooth rows with the labial cusps conical and distally directed. The Y1 bones have a deep embayment for an opercular process.

Few Carboniferous fishes are known from Australia, most of the described taxa being from the Lower Carboniferous fluvial deposits of the Mansfield Group, eastern Victoria (Woodward 1906, Long 1982). The bulk of this material was collected late last century. It was studied initially by McCoy (1890) and later by Woodward (1902, 1906). Woodward assigned almost all of the species to genera known at that time from Europe, especially Scotland, but recent revision of the fauna shows that most of the species represent new genera (Long 1984, unpub. PhD thesis). In addition to the lungfish described in this paper the fauna comprises at least three genera of palaeoniscoids; a large rhizodontiform, *Strepsodus decipiens* Woodward (= *Pycnoctenion decipiens* Vorobjeva and Obrucheva 1977); and, three acanthodians, the commonest being *Gyracanthides murrayi*.

Fish faunas are known from two levels in the Mansfield Group. From the lower level the placoderms *Bothriolepis* spp., *Groenlandaspis* and a phyllolepid genus have been recovered (Long 1983), and hence it is clearly of Late Devonian age. Placoderms are absent from the upper level suggesting that it is post-Devonian in age, a view supported by the occurrence of the fish fauna mentioned above and lycopods of Carboniferous type (Marsden, 1976).

Ctenodus breviceps Woodward (1906) is the only Carboniferous lungfish known from the Southern Hemisphere. It is represented by a single skull roof and a few isolated remains, including toothplates and a partial tail. Although Woodward's sketch of the skull roof is accurate as far as it goes (Woodward 1906, fig. 3), preparation has clarified details of the bone pattern and revealed new data on the course of the laterosensory canals. These features preclude its assignment to *Ctenodus*.

The material is housed in the Museum of Victoria (NMV). Preparation of the holotype by vibrotome and chisel removed some of the matrix obscuring the skull roof bones. At least half the specimen is known only from the impression of the dorsal surface of the skull roof on the rock where weathering has removed the bone. This region of the holotype and the impressions of toothplates were studied from latex casts.

SYSTEMATIC PALAEOONTOLOGY

Class OSTEICHTHYES

Subclass DIPNOI

Genus *Delatitia* gen. nov.

ETYMOLOGY: From the Delatite River which runs through the Mansfield Basin.

TYPE SPECIES: *Delatitia breviceps* (Woodward) 1906.

DIAGNOSIS: Skull roof with a strongly concave posterior margin; B bone strongly waisted posteriorly and equal in length to the paired C bones anterior to it; D small, about three-quarters as long as B; Y1 narrow, L-shaped; Y2 partly but not completely embracing Z laterally; E bones elongate relative to C; I bones with prominent subdermal posterior processes. Occipital sensory line runs posteromesially out of the I-bones. Opercular with strongly developed anterodorsal process. Toothplates flat with more than eight radiating rows of co-linear cusps; outermost cusps form prostrate cones pointed distally. No cosmine on dermal bones.

REMARKS: The above diagnosis distinguishes *Delatitia* from *Ctenodus* by the course of the occipital sensory canal, shape of the Y1 and position of the Z. The toothplates are flat unlike the strongly arched multi-ridged toothplates of *Ctenodus*. The only other dipnoans which have a similar skull roof pattern, with a large B, paired C and small D, but without an isolated bone occupying the K position, are *Tranodis*, *Uronemus*, *Rhinodipterus* and an undescribed new genus from the Late Devonian Mt. Howitt site, Victoria. *Uronemus* is easily distinguished by the absence of toothplates, and any similarity between the roofing bone patterns is considered to be the result of convergence. *Tranodis* is a ctenodid with the Y series reduced and X correspondingly enlarged, an elongated B, and a squat E (Thomson 1965). All these features, together with the position of the occipital commissure, separate it from *Delatitia*. The undescribed new genus from Mt. Howitt differs from all of the above group by having I bones in mesial contact posterior to B. The remaining comparison is with the Late Devonian genus *Rhinodipterus* (as represented by *R. ulrichi*, Ørvig 1961). That species has overall similar proportions of roofing bones, and

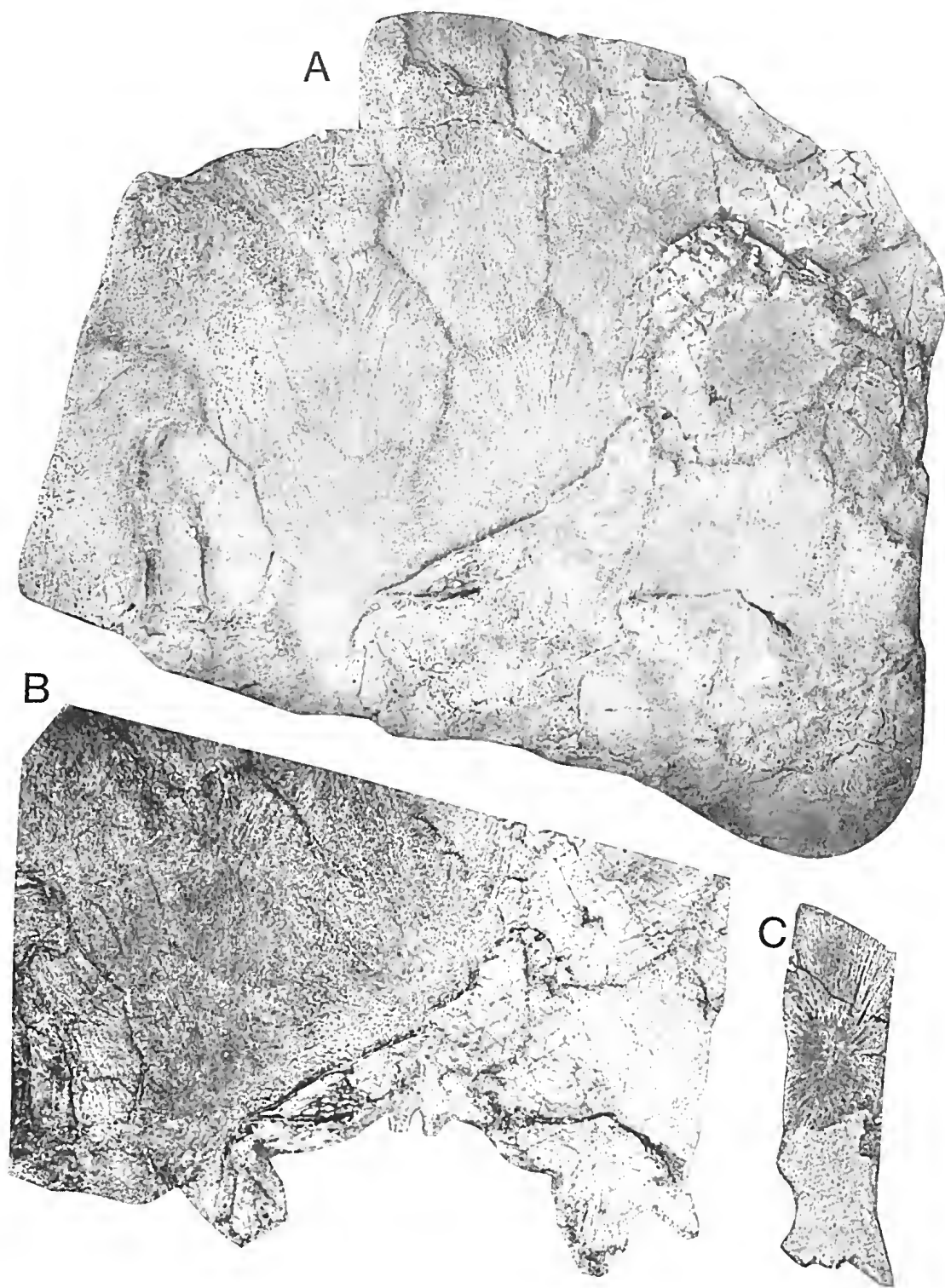


Fig. 1—*Delatitia breviceps* (Woodward) gen. nov. A, B, skull roof of holotype, NMV P10273; A, whitened with ammonium chloride; B, under alcohol. C, isolated E bone, NMV P179625. All natural size.

some individuals have a well-developed D bone. However, it has an ossified snout, eosmine-covered skull, and greatly reduced Y series.

In summary, *Delatitia* is not likely to be confused with any genus with which we are acquainted.

Delatitia breviceps (Woodward)

Figs 1-4, 5E

- 1906 *Ctenodus breviceps* Woodward, p. 15
 1958 '*Ctenodus*' *breviceps*: Hills, p. 91.
 1965 *Ctenodus breviceps*: Gill, p. 17.
 1966 En Australie . . . *Ctenodus*: Lehman, p. 289.
 1967 *Ctenodus breviceps*: Andrews *et al.*, p. 644.
 1976 *Ctenodus breviceps*: Marsden, p. 22.
 1982 A dipnoan (Carboniferous) Long, p. 67.
 1982 ? *Ctenodus*: Long & Kemp, p. 704.
 1984 *Ctenodus breviceps*: Long & Turner, p. 241.

DIAGNOSIS: As for the genus.

MATERIAL: Holotype: NMV P20173, an almost complete skull roof. Other specimens: NMV P10257-P10259, natural moulds of toothplates. NMP 179625, an isolated E bone.

OCCURRENCE: From the upper section of the Mansfield Group near the intersection of Bridge Creek and Broken River, Mansfield, Victoria. Lower Carboniferous.

DESCRIPTION: *Skull roof*. Most of the skull roof, apart from the snout, is known from the impression of the dorsal surface on the rock. The left posterolateral corner has the vertical surface of the bone preserved. Overall the skull roof is gently arched with a shallow depression between the centres of the C and B bones. Numerous closely-spaced, narrow ridges emanate from the ossification centres of bones on the dorsal surface. No eosmine is present. The ratio of posterior breadth of the skull roof/length to the anterior of C is 1.38 for *Delatitia* compared to broader forms like *Ctenodus* in which this ratio is 1.8. The concave posterior margin of the skull roof features well developed subdermal processes on the I bones, with many small irregular processes bordering the whole margin. The lateral margins of Y1, Y2 and Z bones are straight except for a strongly developed notch in Y1 for an anterodorsal opercular process, similar to that found in *Sagenodus* (Watson & Gill 1923, fig. 20). The arrangement of the skull roofing bones is quite similar to that of *Ctenodus* (Fig. 5F) except for the position of the Z bone, which is only partially embraced laterally by the Y2 bone.

Bone B is completely preserved. It is pointed anteriorly and is strongly waisted posteriorly with a narrow posterior margin. The anterior half of B has an irregular suture with the C and J bones. No laterosensory canals or pit-lines pass through B or lie on its surface. Of interest is a pair of small foramina situated on the subdermal posterior fringe of B, possibly for the endolymphatic ducts. The I bones are complete on both sides. The dorsal surface is approximately as long as broad with a well marked anterior point where it meets J and Y1. The ventral surface of I, seen on the left side of the holotype, is marginally broader than long. The occipital sensory-line canal, exposed by preparation, runs

from the posterolateral corner through the centre of ossification to the posteromesial corner. The canal runs off I on the dorsal surface presumably onto the A bone. A short section of the middle pit-line (m.pl) is visible near the lateral margin of I. The C and J bones are completely preserved and are similar to those of *Ctenodus* in their shape, but are slightly narrower in proportion. The anterior margin of J has two concave margins for the X and L bones respectively. Bone X is partially preserved on both sides, being broader than long with a strongly convex posterior margin. Three short straight furrows, taken to be pit-lines, are present in the centre of X. The posteriormost L bone seems to be equidimensional with X, both of these bones being notably smaller than the I, J or C bones.

The Y1, Y2 and Z bones are clearly seen on the right side of the head in dorsal view. Y1 is unusually narrow, almost L-shaped with its longest axis being anterolateral. Y1 has a concave anterior margin, convex mesial margin and a strongly notched lateral margin which received a well developed anterodorsal opercular process. A small furrow, interpreted as a pit-line, is present on Y1. Y2 is almost equal in area to Y1 but is a straight, narrow bone, being almost as long as I or J but only half the breadth of these bones. A short sigmoid pit-line runs across the Y2-I boundary. Z is broader than long with convex anterior and mesial margins. The main lateral-line canal exits Z at the lateral section of the posterior margin and goes off the skull roof in a posterolateral direction.

D is nearly complete, missing only its anteriormost section. As there is inwards curvature of the lateral margins close to where the bone is cut off it is assumed to be almost complete. Bone D is ovate in outline as in *Ctenodus* but is slightly smaller relative to the size of B. Only the extreme posterior ends of the E bones are seen in the holotype, contacting the D, C and L bones. An isolated E bone (Fig. 1C) is long and narrow, having a breadth/length index of 28, quite unlike the E bones of *Ctenodus* species (*C. cristatus* E bones B/L = 47, *C. interruptus* E bones B/L = 39). The anteromesial corner of the E bone diverges slightly from the long axis of the bone, suggesting the presence of a small F. The centre of ossification of E is slightly anterior of centre.

A restoration of the head is given in Fig. 3. The proportions of the snout are conjectural, being based mainly on the length of the lingual ridge of the mandibular toothplate and the length of the isolated E bone.

TOOTHPLATES: Three imperfect toothplates from the Mansfield Group are presumed to belong to *Delatitia* as this is the only dipnoan known from the fauna. They are all preserved as natural moulds devoid of any bone or dentine. Woodward figured and described these specimens as anterior prepectoral spines of the acanthodian *Gyracanthides murrayi* (Woodward 1906, pl. 1, figs 3-6), but Hills (1958, p. 91) recognised them as dipnoan toothplates. Specimen NMV P10257, is the most complete individual, but it lacks the distal ends of most of the ridges and the heel of the plate, so that the overall form cannot be determined. The first ridge is dispropor-

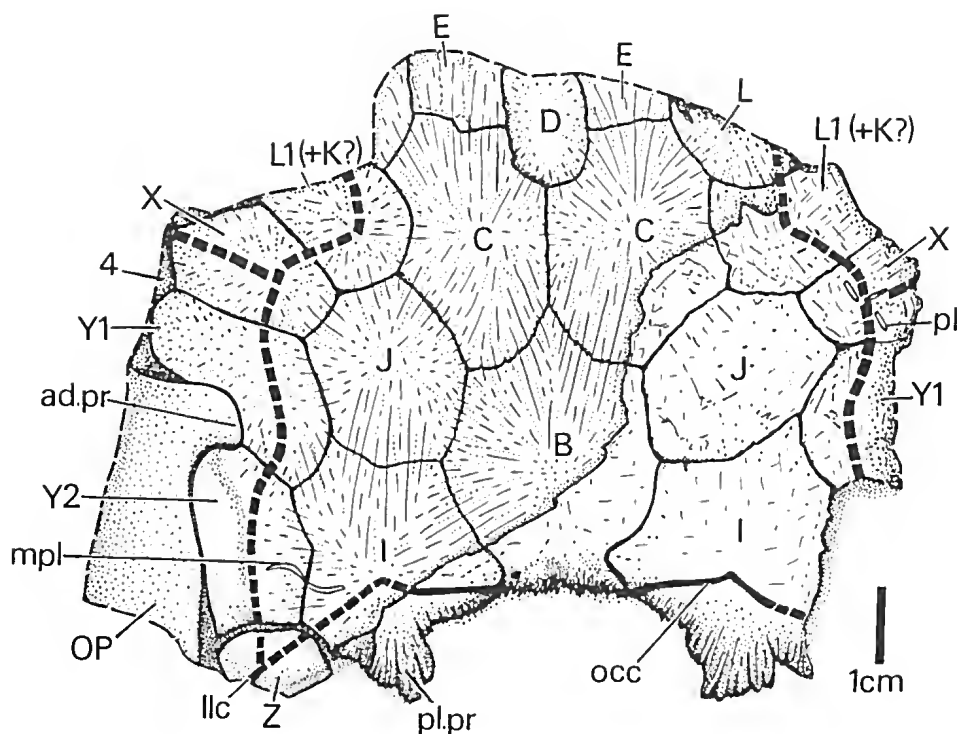


Fig. 2—*Delatitia breviceps* (Woodward) gen. nov. Skull roof of holotype, NMV P10273. Broken lines indicate presumed course of laterosensory-canals. Abbreviations: B, C, D, E, I, J, L1, L2, X, Y1, Y2, Z, 4—bones of the skull roof; ad. pr, anterodorsal process of opercular; llc, main lateral line canal; mpl, middle pit-line; oec, occipital sensory-line canal; OP, opercular; pl, pit-lines on the X bone; pl.pr, posterior subdermal process of the I bone.

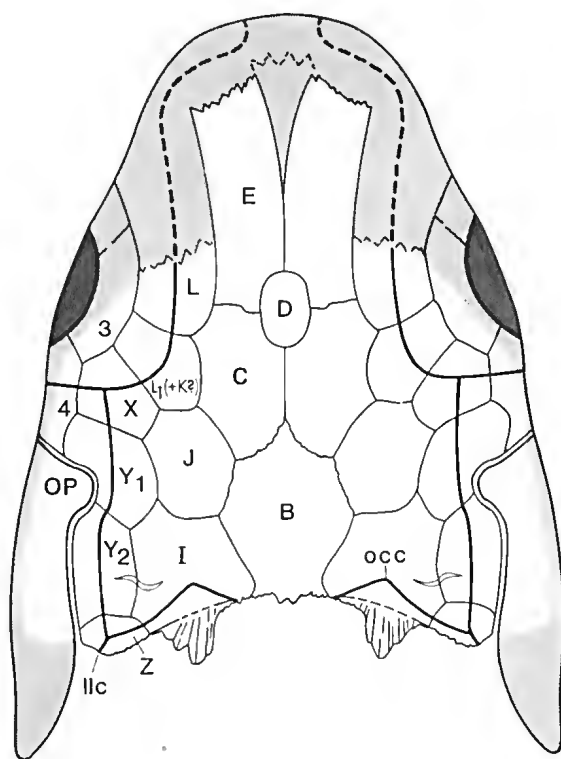


Fig. 3—*Delatitia breviceps* (Woodward) gen. nov. Attempted reconstruction of the head in dorsal view. Light stipple indicates areas which are not known from the material. The shape of bones 3 and 4 is based on the lateral margins of Y1 and X. Laterosensory canals shown as heavy black lines.

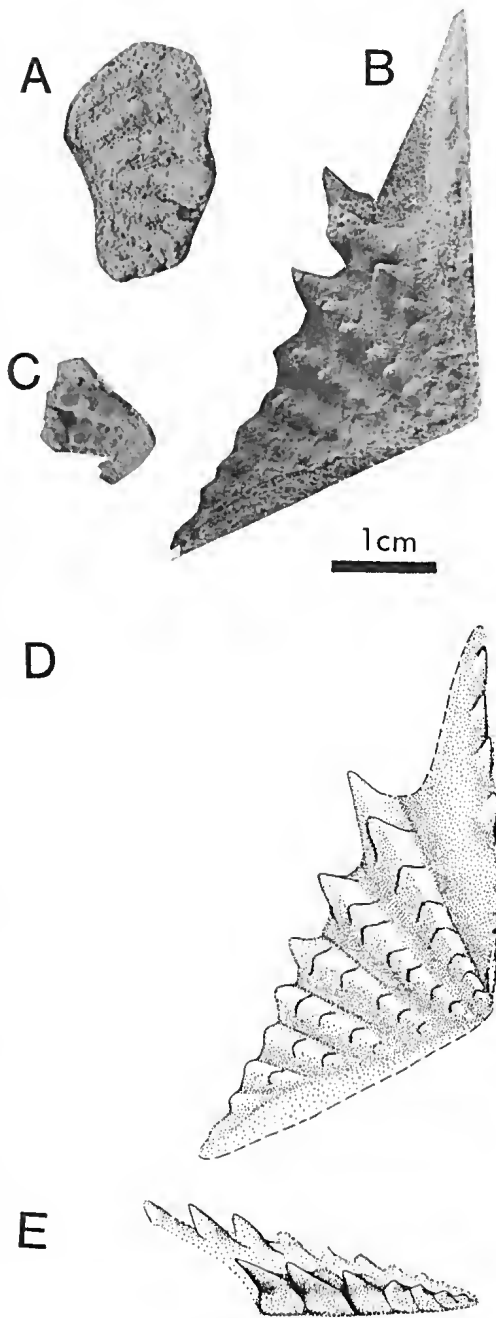


Fig. 4—*Delatitia breviceps* (Woodward) gen. nov. Toothplates. A, NMV P10258. B, NMV P10257. C, NMV P10259 (all $\times 2$). Latex casts whitened with ammonium chloride. D, attempted restoration of the left mandibular toothplate, based on NMV P10257. E, posterior oblique view of first two tooth ridges of NMV P10257. Partially restored outlines are shown by broken lines.

tionately longer than the posterior ridges and is separated from the second ridge by an unusually wide furrow (Fig. 4).

The mandibular toothplate of lungfishes can be distinguished by the longer first ridge which may curve mesially at its anterior extremity, and by being narrower in overall shape (e.g. *Rhinodipterus*, Gross 1956, Ørvig 1962; *Dipterus*, Jarvik 1967). NMV P10257 is identified as a left mandibular toothplate. It has a very long lingual ridge which has slight anteromesial curvature, and diverges from the second ridge at an angle of $ca\ 22^\circ$. There are at least eight teeth on each of the second and third ridges, diminishing to six and five on the fourth and fifth, but all the distal teeth may not be preserved. The first row has few anterior teeth preserved, these being long, conical to triangular prismatic in form, and directed anterolaterally. The teeth of the remaining rows have relatively flat sides meeting at a median crest so that all the teeth coalesce to form a co-linear ridge. The outermost teeth diverge from this ridge to point laterally and, in some instances, for example between the second and third cusps of the second row, there is a recess between the vertical sides of the individual cusp bases. Growth of each cusp over the preceding cusp can be barely seen by traces of growth lines. The other toothplates (NMV P10258, P10259) are incomplete and more worn than NMV P10257 but show the same type of array of cusps which have flat sides and coalesce into a median crest (Figs 4A, C).

DISCUSSION

In the overall roofing bone pattern, this new genus has obvious similarities to *Ctenodus*. The two genera have the same number of roofing bones disposed in approximately the same way, and they share a distinctive shape of the lateral bone canals from X to L. However, *Delatitia* retains two important primitive characters lost in *Ctenodus*—the larger Z which is not integrated into the skull roof, and the passage of the occipital commissure through a loosely attached bone A. *Conchopoma* is the only other post-Devonian genus with a similar bone Z and the occipital commissure in a loose bone A, but that genus has a denticulate palate and has lost its C bones (Schultze 1975). The similarities with *Delatitia* are of no significance in interpreting relationship. In the shape of Z and the position of the occipital commissure, *Delatitia* is similar to several Late Devonian genera (Fig. 5A-D), among which *Rhinodipterus* of the *R. ulrichi* type has the most comparable roofing pattern. As Miles (1977, p. 241) has indicated, many specimens of that species retain a D bone. However, there are several major differences between *R. ulrichi* and *D. breviceps*—*R. ulrichi* has cosmine-covered bones, an ossified snout, and a single Y bone, the first two features being primitive and the third being advanced. The roofing bone pattern of *D. breviceps* also has several features in common with the Late Devonian *Scaumenacia curta*, particularly the squat B bone, the Y2 notched to receive the process on the anterodorsal corner of the opercular, and the unintegrated Z bone.

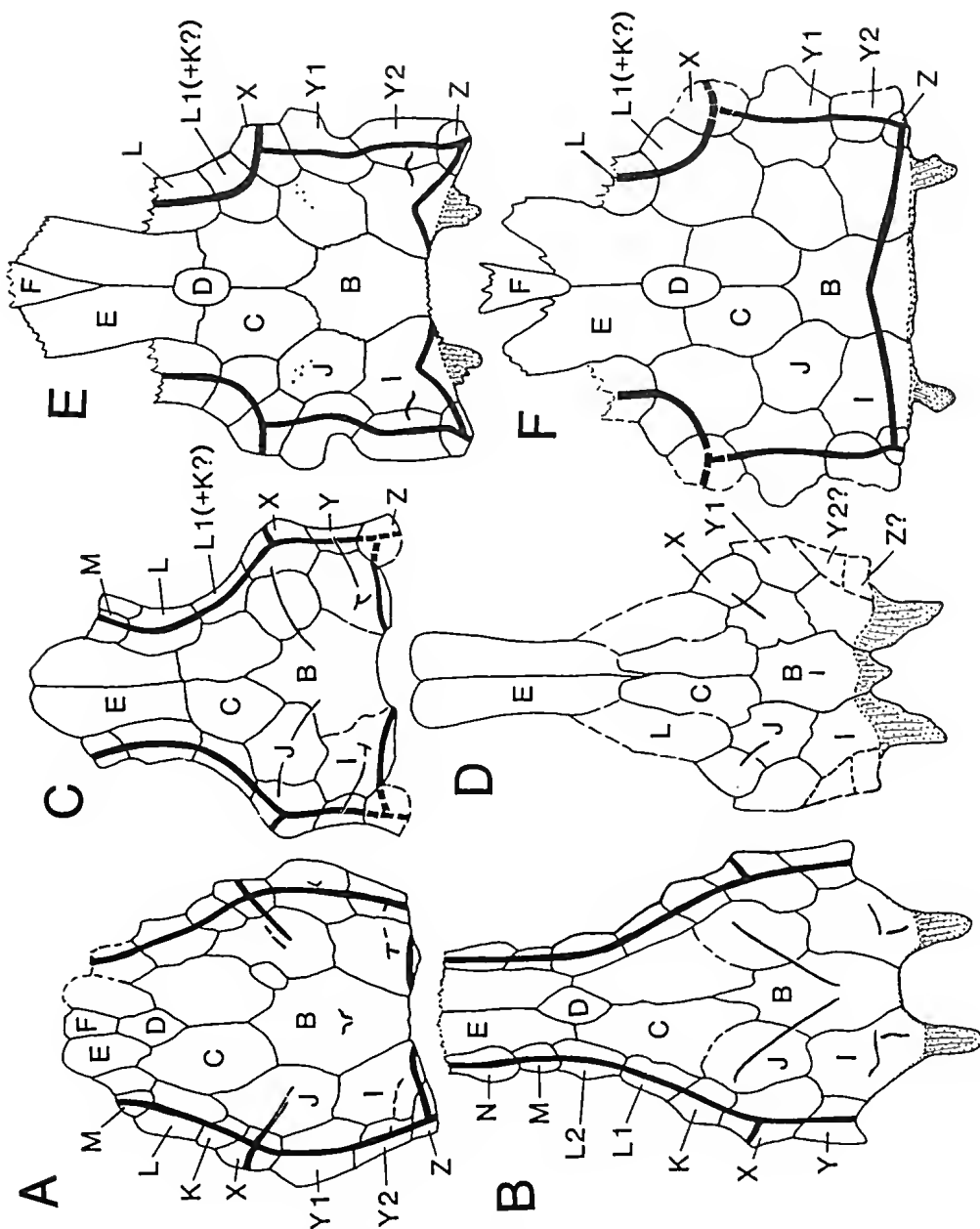


Fig. 5—Comparison of certain Palaeozoic dipnoan skull roof patterns. Laterosensory canals in heavy black lines, broken lines where uncertain. A, *Chirodipterus australis* (from Miles, 1977). B, *Rhinodipterus secans* (from Thomson and Campbell, 1971). C, *R. ulrichi* (from Ørvig, 1961). D, *Oerwigia nordica* (modified from Lehman, 1959). E, *Delatitia breviceps* (Woodward) gen. nov. F, *Ctenodus cristatus* (from Westoll, 1949). Not to scale.

Moreover, the cosmine has been lost. We note that despite the large number of specimens available, bones D and F have not been recorded in *S. curta*, and in these respects it is more advanced than *Delatitia*. *Sagenodus* also has a well developed notch in Y1, but the absence of C bones, the integrated Z and the occipital commissure in B, all indicate that it has evolved independently, well beyond the stage reached by *Delatitia*.

The toothplates are of value in determining relationships. Important features are the elongate lingual ridge, the closely-packed teeth along the main parts of the ridges, and the recumbent conical distal teeth. These features are not characteristic of *R. ulrichi* or *S. curta*, though they are known in *Ctenodus* and in a number of isolated Late Devonian toothplates from Antarctica housed in the Australian Museum, Sydney (specimen numbers 54318, 54320, 54322, 54323). The lower toothplates of *Ctenodus* are strongly convex in profile whereas those of *Delatitia* are flat, but this difference is not of great significance. *Tranodis*, considered by some workers to be a ctenodid, apparently differs from both *Delatitia* and *Ctenodus* in the absence of Y2 and the shape of the whole X-L region. Such a placement for *Tranodis* seems improbable in view of the other features of the genus, especially the structure of the anterior part of the roof and the toothplates. The posterior part of the skull roof of *Tranodis* requires rather study.

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SEA LEVELS AND ABORIGINAL OYSTER MIDDEN AT LAKE CONNEWARRE, VICTORIA, AUSTRALIA

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ABSTRACT: Lower Pliocene basalt flows have created a series of lakes and swamps near the mouth of the Barwon River. No measurable earth movements have occurred since the Last Interglacial, because widespread estuarine beds of that age are horizontal, and their surface stands at +7 m as on the stable Warrnambool platform. Around the lakes and swamps are mid-Holocene terraces that contain mollusc species requiring greater salinity, including oysters. These emerged beds are evidence of a higher sea level.

It has long been held that Aborigines harvested oysters only in East Gippsland and along the east coast of Australia. In this paper a large oyster midden about 1 m thick on Campbell Point in Lake Connewarre is described. Others in the same district occur at North Shore and Batesford, and another occurs near Warrnambool in S.W. Victoria.

At a depth of 0.76 m (not the base) a large *Anadara* valve dated 5270 years B.P. (corrected), the time of the mid-Holocene higher sea level, was collected; while at the surface of the Campbell Point midden an oyster valve dated 3620 years B.P. (corrected) was found. The latter marks approximately the time when oyster harvesting ceased after a long tradition of some two millennia. As the whole fauna requiring a higher salinity than now died out at about this time, the change is attributed to fall in sea level.

When Coulson (1933, 1935) described the sediments, fossils, biology and archaeology of the Lake Connewarre-Reedy Swamp system near the mouth of the Barwon River in Central Victoria, he became the first to describe in detail a Quaternary formation in Victoria. To understand his contribution it is necessary to review the background against which it was written. Scientific attitudes in the 1930s were still those inherited from the United Kingdom, where most scholars had their origins, and where nearly all Ph.D. degrees were taken. Charles Darwin said that the Diluvium (virtually the Pleistocene) was "never studied" until the Ice Age was discovered (F. Darwin 1887, p. 250). No comparable glacial deposits occur in Victoria, so it was common to neglect the Quaternary. A comment often heard in the 1930s in Victoria was "Geology ends with the Pliocene."

Assumptions accepted without question at the time of Coulson's writing, but now known to be erroneous were:

1. *Eustasy does not occur.* Although the idea was put forward in 1842, it was slow of acceptance. The emerged shell beds at Lake Connewarre and the deep channel under the Moolap flats were explained by earth movements, as were the deep channels cut by rivers during low sea levels. Coulson could explain such features only by folding and warping.
2. *Laterite does not occur as far south as Victoria.* Thus Coulson had difficulty explaining the extensive ironstones in his study area.
3. *Aborigines in central Victoria did not harvest oysters.* At that time the antiquity of the Aborigines was surmised to be about 4000 to 6000 years at the most. They were considered to have had one culture, and not a series of cultures as had been described in Europe. Coulson's record of two oyster middens at Lake Connewarre was not accepted. It was commonly thought that he had confused emerged shell beds

with middens, which was then a common error (hence Gill 1950). However, to our knowledge, no one checked his claim in the field.

ORIGIN OF LAKE CONNEWARRE

Coulson (1933, 1935, 1938, 1977) showed that the complex of flood plains, lakes and swamps that characterizes the course of the Barwon River from Geelong to the sea is due to a series of lava flows. It is now known that the complex is also due to eustatic changes of sea level that have alternately caused the sea to invade the area, and then by retreating to lower base level so as to cause overdeepening of stream channels. The latest retreat of the sea that has shallowed the lakes and left terraces around them was not caused by earth movements, because the extensive Last Interglacial estuarine beds (Gill and Collins 1983) are at the same +7 m level as on the stable Warrnambool block.

ORIGINAL CONDITION OF LAKE CONNEWARRE

To understand the facies changes in Lake Connewarre, it is helpful to learn what the area was like under natural conditions before European occupation. Frances Balfour-Melville (1984) lived in the area in the second half of last century. Her father bought land on the lake about 1863 and built a homestead called "Toorang", where she lived until married in 1890. An illustration in her paper shows well-vegetated land bordering the lake north of Campbell Point (Fig. 1). The water was shallow with a black mud floor. Regattas were held there until mud deposition due to clearance of the Barwon catchment and mining activities in the headwaters of the Leigh River (P. F. B. Alsop pers. comm.) caused shallowing and increased weed growth, which forced abandonment of the regattas. Coulson (1935, p. 2) states that when he was working there the depth of water in the middle of the lake was "four feet" (1.22 m) but originally was "seven feet" (2.13 m). In the half cen-

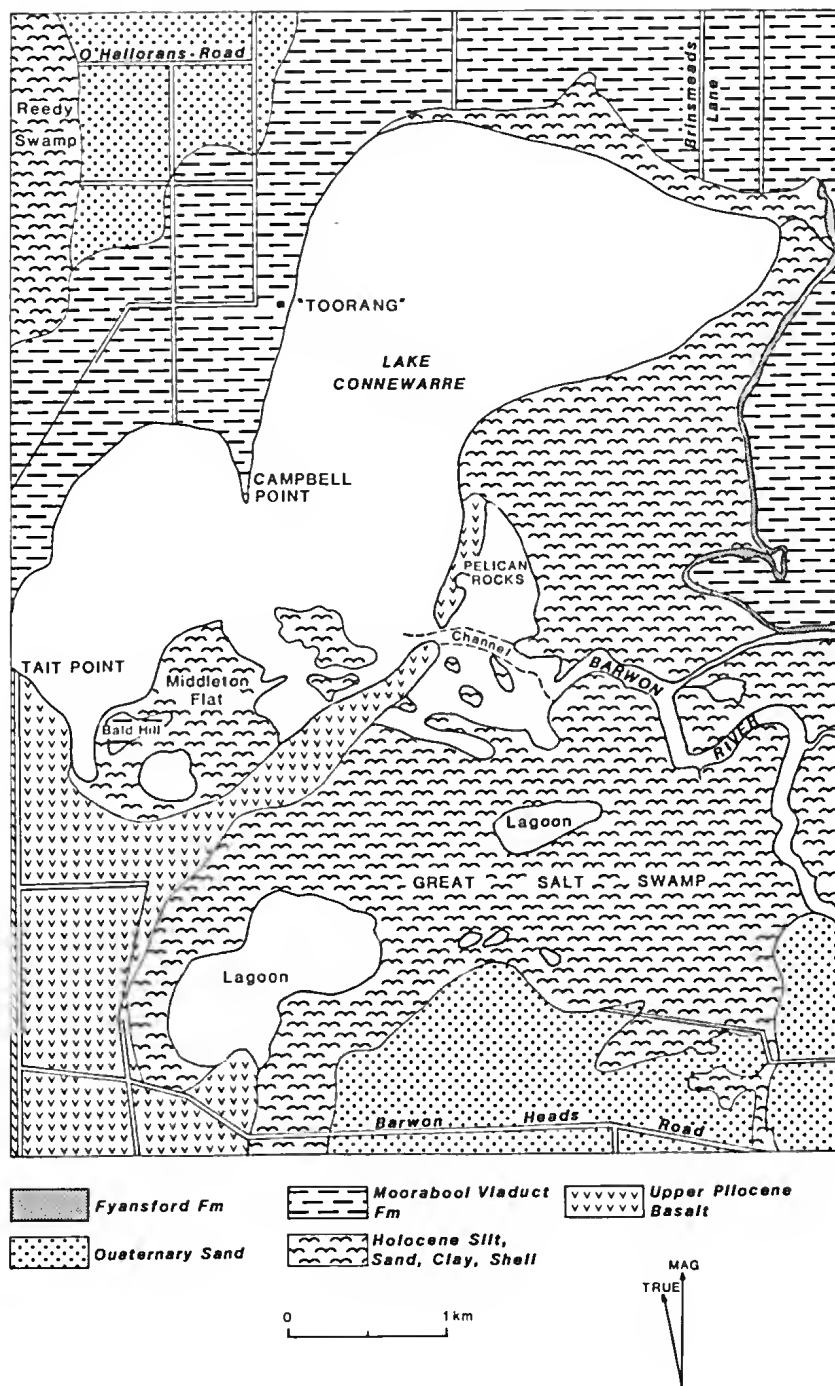


Fig. 1—Map of the Lake Connewarre area, adapted from Coulson (1935).



Fig. 2—Telephoto of the east side of Campbell Point, Lake Connewarre, Victoria. The top of the rounded hillock at the tip is the oyster (*Ostrea*) midden with *Anadara*. Note the emerged terrace of mid-Holocene age formed when sea level was higher. The point consists of Moorabool Viaduct Formation (late Miocene). The rocks outcropping in the lake are late Miocene. E. D. Gill photo.

tury since Coulson did his extensive work on Lake Connewarre, further deposition has occurred. Coulson gave the tidal range as “30 inches” (0.76 m). Campbell Point is 8 km in a direct line from the sea at Barwon Heads, and much further along the waterway, which has changed from time to time.

EXTANT AND MID-HOLOCENE FAUNAS IN LAKE CONNEWARRE

Coulson (1933, p. 16) listed the molluscs found living then in the Barwon River-Lake Connewarre system. The facies range from the open sea rocky substrate species at the mouth (e.g. *Subnivalia undulata*) to estuarine species (e.g. *Notospisula parva*). Lake Connewarre is presently brackish, but almost fresh during floods. With up to 1 m of mud deposited on the floor since European occupation, it is difficult to collect the mid-Holocene fauna, but at some sites shells have been washed out of the terrace sediments, and are found on the beaches. For example, on the lake shore at the end of Brinsmead Lane, shells collected included *Anadara*, *Ostrea*, *Katelysia*, *Cabestana*, *Cominella*, *Bullaria*, *Nassarius*, *Polinices* and *Velacumantus*. Bay and inlet conditions must have obtained for genera like *Cabestana*, *Ostrea*, *Katelysia* and *Cominella* to thrive. The relict cliff at the end of Brinsmead Lane consists of the Moorabool Viaduct Formation, so the shells have not come from there, and must be from the low terrace on which the boat ramp and other facilities are constructed. The

geological maps (Coulson 1935, Spencer Jones 1963) show the wide extent of this terrace, which is part of the former lake floor. The terrace occurs on both sides of Campbell Point (Figs. 2, 3), and is a function of the widespread mid-Holocene higher sea level, as studied in detail at Warrnambool and Seaspray (Gill and Lang 1982).

Care has to be taken in interpreting faunas from this terrace, because in some places the terrace has been formed in front of a cliff of similar sediments with the same species, but Last Interglacial in age, so that Last Interglacial fossils can mingle in the terrace with Holocene specimens of the same species.

For example, *Anadara trapezia* shells excavated from the Holocene terrace at the west end of O'Hallorans Road in the N.E. sector of Reedy Swamp gave a false radiocarbon date. Five unworn and chemically reduced shells of this species which could not be distinguished from one another in preservation were found to be partly Holocene and partly Last Interglacial because they dated $16\,580 \pm 190$ years b.p. Three shells were used for the assay, and Dr. M. Barbetti who made the dating (SUA-2072), pointed out that “one Holocene valve about 7 200 years and two Last Interglacial valves would account for the above result”. At this site there is a Last Interglacial cliff behind the Holocene terrace (Gill and Collins 1983) with oxidized *Anadara* shells. Apparently in these very low energy waters, *Anadara* shells were washed out of the cliff and included in the black



Fig. 3—Telephoto of the west side of Campbell Point, Lake Connemara. The top of the domed hillock at the tip with the tree shadow on it is the oyster (*Ostrea*) midden with *Anadara*. Neither genus now lives in the lake. Note the equal development on this side of the point of the mid-Holocene terrace formed by a higher sea level. The trees near the shore are paperbarks (*Melaleuca*); they once lined the entire shore, so the midden site under natural conditions was not as bare as now. E. D. Gill photo.

Holocene mud which chemically reduced them so that they could not be distinguished visually from the Holocene ones. Because of the low energy conditions, none of the shells is worn.

Although Reedy Swamp (formerly a lake) is further from the sea than Lake Connemara, its mid-Holocene fauna has the same bay/inlet genera found in Lake Connemara. A collection was excavated at the south end of Whites Lane, where there is no cliff of Last Interglacial sediments from which re-cycled fossils could come.

EFFECTS OF SEA LEVEL CHANGES

The peak of the last rise of sea level was about 6000 years ago in Australia (Gill 1971, Gill and Hopley 1971, Thom and Chappell 1975). Precision boring and surveying at Warrnamboul in Western Victoria and Seaspray in Eastern Victoria (Gill and Lang 1982) has shown that the peak sea level was at about +2 m approximately 6000 years ago, and that this was followed by an oscillation at about +1 m approximately 4000 years ago. That this latter was an oscillation and not simply a fall in sea level is shown by the fact that the 6000 year bed was eroded before the 4000 year one was emplaced (c.g. Gill and Lang 1982, fig. 10). The 6000 and 4000 year phases have been recognized in a number of places.

With the anthropogenic mud bed added since European occupation, it is difficult to sample the underlying shell beds at Lake Connemara. So in order to date when the sea retreated enough from the lake to cause the

demise of the *Ostrea* and *Anadara* beds a different approach was devised, viz. to determine when the Aborigines ceased harvesting these molluscs from the lake.

Ostrea-Anadara MIDDEN, CAMPBELL POINT

Campbell Point, where in 1935 Coulson recorded an oyster midden (which also contains some *Anadara*), is a narrow promontory of Moorabool Viaduct Formation sediments (clayey sand). Coulson (1935), Mulder (1904) and Stach (1933) have recorded Tertiary marine fossils at this locality, preserved as casts and molds, from about "eight feet above high water mark." The tip of Campbell Point is an isolated circular hillock with cliffed sides standing well above the lake (Figs. 2, 3). It was an island or almost an island when the sea stood 2 m higher. The top of the hillock is a midden consisting of vast numbers of oyster shells, and also many *Anadara* shells, but *Ostrea* predominates. Charcoal is present and a pebble tool and two pieces of flint were found. It is an ancient midden because cliffing has made the sides of the midden continuous with the profile of the hillock. There is also some weathering and juvenile soil formation at the surface. The midden represents a long period of time because it is at least a metre deep and has become compacted. These conclusions were tested by radiocarbon dating.

We were assisted by the owner of the property, Mrs. Nancy Matthews and her son, Mr. Murray Matthews,

who said that when digging rabbits out of the midden, he sank a hole "three feet deep" without reaching the bottom. As further evidence of midden structure, it can be seen that the shells are in relatively random orientation, and not in the flat position of shells in water-deposited beds. The midden is too high to be a Holocene marine deposit. There has been human selection of the shells, as they are all of edible sizes and of virtually two species only. Search found only one shell of any other species, viz. a *Pleuroploca*.

From the point of view of sea level studies, this midden provided an opportunity to determine when the Aborigines were last able to harvest oyster shells in Lake Connewarre.

RADIOCARBON DATINGS

1. One large *Anadara* valve from approximately 0.76 m deep in the midden dated 5720 ± 80 yr b.p., or 5270 yr B.P. (SUA-2153) (b.p. in lower case indicates an uncalibrated date; subtracting the seawater age of 450 years gives 5270 yr B.P.).
2. One large *Ostrea* valve from just below the grass dated 4070 ± 80 yr b.p., which is 3620 yr B.P. (SUA-2152). Samples were collected by L.N.L.

Thus *Ostrea* and *Anadara* flourished during the peaks of higher sea level about 6000 and 4000 years ago (Gill and Lang 1982) when the sea had access to Lake Connewarre. After some two millennia (the C14 date is not of the base of the midden), the Aborigines ceased their very long tradition of harvesting oysters. Some explanation is necessary. Not only *Ostrea* but the whole fauna of molluscs requiring a higher salinity disappeared from the lake. It has already been shown that earth movements are not the cause. Nor is change in the sedimentary regime, because this is held tightly within the bounds of the basal flows. Retreat of the sea is the explanation and 3620 yr B.P. dates the demise of the oyster population because Victorian Aborigines were not a sea-going people, so did not harvest them from offshore.

Coulson (1935) recorded a second oyster midden at Fishermens Point, but this appears to have been destroyed by cultivation.

Ostrea/Anadara MIDDENS AT BATESFORD AND NORTH SHORE

Australian Portland Cement Limited, who work the quarry in Tertiary limestone at Batesford, N.W. of Geelong, kindly permitted us to quote a report prepared for them by the La Trobe University Archaeological Consultants (1982). Ten Aboriginal Sites were found on the company's property, one of which contained *Ostrea* and *Anadara* along with the core tool implements that indicate antiquity. It is the only midden of the group situated west of the Moorabool River. The estuary of Cowie Creek in Geelong was the nearest place these shellfish could be harvested. During the higher sea level they also occurred in Hovell Creek a little further north (Gill 1972). Of the many shellfish available, the

Aborigines harvested only two species. Meehan (1982) describes how contemporary Aborigines of the Blyth River in the Northern Territory collect 29 species including *Ostrea* and *Anadara*. However, in the same area are relict middens belonging to the "Dreaming" that contain many fewer species with *Ostrea* and *Anadara* absent.

In Moorpanyal Park, North Geelong, on the cliff top opposite the corner in the Espanade, there is a large midden with *Ostrea*, *Anadara*, *Mytilus* and *Eumarcia*. This midden has not been dated and the shells come from Corio Bay which is deeper than Lake Connewarre, and so has not been affected in the same way by fall of sea level.

ABORIGINAL OYSTER HARVESTING

Until recently Aboriginal oyster middens were believed to be limited to east Gippsland. "P. J. F. Coutts has investigated and dated middens containing *Ostrea* at Wilsons Promontory, while K. Hotchkin has mapped and dated *Ostrea* and *Anadara* middens at Jack Smith Lake" (Hotchkin in litt.). So the record of oyster middens in the Geelong district is of great interest, but there is also a record from the Warrnambool district in S.W. Victoria. Samuel Hannaford (1860) recorded a mass of oyster shells on top of a hill at Tooram, on the Hopkins River estuary 9 km from the mouth. Dr. John Sherwood of the Warrnambool Institute of Advanced Education and E.D.G. had no difficulty locating the site, and there was evidence of Aboriginal occupation, but the midden had been destroyed by cultivation like that on Fishermens Point at Lake Connewarre. Mr. B. Logan, the property owner, said he had been told about this oyster midden, and another on the opposite side of the river, but he had not seen them himself. The Aborigines who harvested the oysters could have obtained them only from the river. So Sherwood and Gill, assisted by C. Magilton, tested a low terrace below the hillock midden site. An auger hole located a shell bed with oysters at a depth of about one metre. The shell bed was then seen at about the same depth in the banks of the Lake Gillcar drain that enters the river nearby. This bed also had oysters, as did the drain spoil heaps, and must be the source of the oysters utilized by the Aborigines. The shells were dated 5900 ± 70 yr b.p. or 5450 yr B.P. (SUA-2203). For oysters to grow in the river 9 km from the present mouth would require a higher sea level.

Thus Aborigines in the past harvested oysters in Central and Western Victoria, but have not done so in recent times. Holocene oyster beds are common around the coast of Victoria, so a search of such areas for ancient Aboriginal oyster middens could be rewarding.

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THE MANAGEMENT OF SCIENCE

Seminar held at the Royal Society of Victoria, 7th November, 1984

FOREWORD

The papers presented at this seminar are published with only minor editorial amendment. They are in essence speakers' notes. The decision by the Council of the Royal Society to publish these papers and thus extend the communication of the thoughts in them, is significant. It signals the awareness of Council of the urgent need for scientists to understand the role of the manager and thus be capable of managing science, so that it is more responsive to the economic and social needs of the community. The time is long past when the management of science can be seen as a chore which many scientists grudgingly accept as an interference with a legitimate career.

R. H. Taylor
Assistant Director-General, Department of Agriculture, Victoria
Councillor, Royal Society of Victoria

THE TECHNOLOGIST AS MANAGER FORMULA FOR FAILURE?

By J. G. ONTO

Head, Department of Management, David Syme Business School, Chisholm Institute of Technology

Thomas A. Edison never forgot his role as a business man. The profit motive was an essential part of his temperament. Once he said practically to a friend, referring to a newspaper article which discussed him as a scientist, "That's wrong. I am not a scientist. I am an inventor. Faraday was a scientist. He didn't work for money, he hadn't the time. But I do. I measure everything I do by the size of a silver dollar. If it don't come up to that standard, then I know it's no good."

A botanist found a beautiful plant by the wayside. He sat down to analyse it. He pulled it apart and examined every part under a microscope. When he had finished, he could tell the colour of the flower, its classification, and the number of stamens and pistils and petals and bracts, but the life and the beauty and the fragrance had gone.

INTRODUCTION

My purpose in this paper is to get you thinking; to stimulate you to confront the issues relating to the technologist in the management role and act as a catalyst for subsequent discussions which might lead to strategies for better equipping the technologist for the management task. I would like to approach the discussion by posing two hypotheses; an approach which should be empathetic to the *modus operandi* which many of you use in your own occupations.

Hypothesis 1

That technologists are ill equipped by virtue of their training, values and other personality characteristics for the role of management.

Hypothesis 2

That the role of management, in the technological context, is in, and of itself, a precondition for failure in the job.

These hypotheses, supportable or otherwise, would not be worth discussing but for the fact that a large proportion of engineers and scientists, at some stage of their careers, will be in a management role and that proportion is increasing. We don't have statistics for the Australian scene but the US picture indicates that over 70% of engineers are working in jobs with a significant management content by the time they are in their mid-to-late forties. A related point is that, although the technologist manages primarily other technologists, in-

creasingly, there is evidence that he/she will move into the general management role. Again, quoting US experience, it is estimated that in the '80s, more than 50% of chief executives will be holding engineering degrees.

HYPOTHESIS 1

That technologists are ill equipped by virtue of their training, values and other personality characteristics for the role of management.

The training orientation of most technologists focuses heavily on technical subjects. Where they are exposed to other material, they often resent this, seeing it as a digression, or worse still, a soft option, not requiring the same commitment as their main stream studies. An increasing number of applied science and engineering undergraduate programs are incorporating management studies but in most cases, I consider this largely a waste of time.

The motivations for this broadening influence are quite diverse and may include any or all of the following:

1. It's a break from the rigors of the technical studies.
2. The incorporation of management or business studies may make the program more attractive to potential students. This view derives from the observed success and growth of business studies programs.
3. There is someone on the teaching staff who once did a course in administration and would like to teach management.
4. There is someone on the staff who is finding the maintenance of currency in their technological area too difficult and would like to find something apparently less demanding.
5. Last and not least, incorporation of management-related units is perceived to be educationally desirable. The most material evidence of this motive is the use of management experts from outside the technology faculty to teach the material required.

Having said this, we should be quite clear that management training is required for technologists, particularly those who aspire to management roles. The question is, when? I have some doubts that the undergraduate program is the appropriate place, or course. I do recognise that the undergraduate program heavily emphasises the development of analytical skills. Further, these very skills which will probably determine

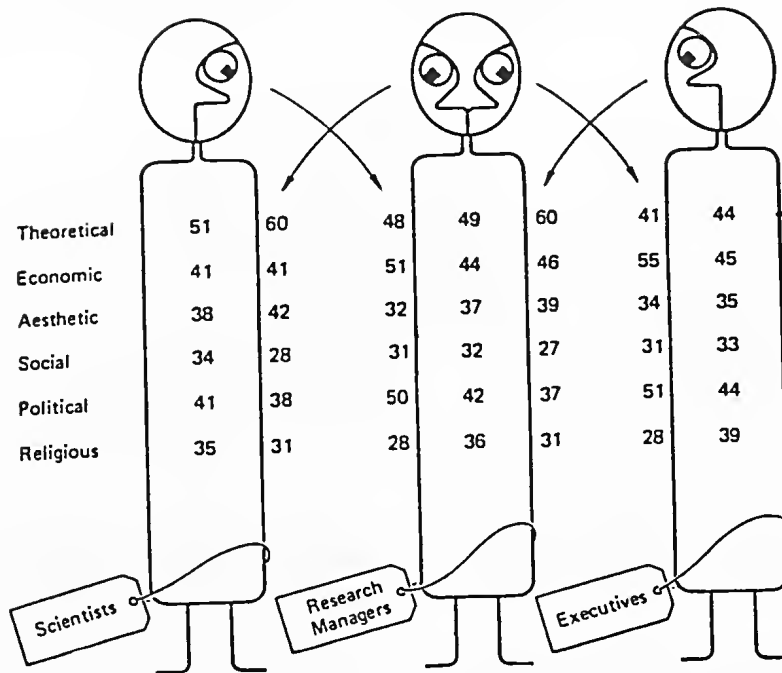


Fig. 1—Values of Scientists, Research Managers and Executives—Self Ratings Versus Ratings Expected From Others (Guth and Taguiri, 1965)

the success of the technologist, are counterproductive to effectiveness as a manager.

The training of engineers and scientists typically emphasises the reduction of all problems to terms that can be dealt with by objective measurement and established formulas based on predictable regularities (Badawy, 1982).

Peter Drucker highlighted the dangers of this orientation many years ago. "I am a figures man, and a quantifier, and one of those people to whom figures can talk . . . Reports are very comforting to me; they tell me a great deal. But they have also misled me often enough to make me realise that unless I go out and gain understanding, I may be acting on yesterday, even though the information is up to date."

Turning to personal values, we find considerable support for the view that there are differences in values between those in managerial roles and other organisation members. For the purposes of this discussion, a value is defined as a tendency to prefer certain states of affairs over others. Values may be conceived in a systems framework and one's value system defined as "a relatively permanent perceptual framework which shapes and influences the general nature of an individual's behaviour."

In a landmark study, Guth and Taguiri (1965) studied the values of nearly 1,000 scientists, research

managers and executives. Using the Allport, Vernon and Lindzey instrument they measured the values of these groups and the results are summarised in Fig. 1.

Subsequent research has tended to support the view that value systems influence occupational choice and direction. Although the difference in value systems might be interesting, the key question, of course, is, are they relevant? Management has been defined as "getting things done with and through others." The process of management is often described as "planning, organising, directing and controlling resources in order to produce goods and services." We might elaborate the technology managerial role as "planning, organising, directing, and controlling the activities of engineers, scientists, designers etc. to achieve desired goals in technologically related functions."

An increasing amount of research recently has attempted to address the question of management competencies. Without exploring this in any depth, we can, with some confidence say that there is a strong requirement for interpersonal skills, a preparedness to acquire and use power, and an orientation toward the achievement of measurable results and pragmatism. This implies that people who are likely to derive satisfaction from the managerial role are most likely to have consonant value systems. And indeed the research supports this view. Conversely, those with different value

TABLE I
TECHNICAL MANAGEMENT AND TECHNICAL SPECIALIST—SOME ROLE DIFFERENCES*

Technical Management	Technical Specialist
Counsels, guides, directs people	Is consulted by people
Is sensitive to feelings, attitudes	Is intuitive, creative
Evaluates people's performance	Evaluates data systems or methods
Forecasts, analyzes, controls costs	Technical performance outranks cost
High verbal skill required	High analytical skill required
Transmits and enforces policy	Logic outranks conformity
Directs what methods to use	Determines operational methods
Makes decisions from insufficient data	Seeks additional data
Accepts organizational hierarchy	Accepts hierarchy of truth
Seeks relationships to business goals	Seeks relationships among technical facts

* Source: Balderston, J. L. 1978. Do You Really Want to Be a Manager? *Journal of the Society of Research Administrators* 1X, 4.

systems, particularly values usually found in association with technology, are likely to experience frustrations and tensions when called upon to fill a role which requires behaviour which is dissonant with their values.

HYPOTHESIS 2

That the role of management, in the technological context, is in, and of itself, a precondition for failure in the job.

If Hypothesis 1 has any validity, and please remember I am offering hypotheses, not facts, or even theories, then we already have support for this second postulate. I have already suggested that there is an intrinsic conflict between the values typically held by scientists and managers, and their educational orientation. I now want to suggest that this conflict is emphasised by the role prescription of the scientist and manager.

The problem which is enunciated here is not typical to scientists, but is generic to any group of professionals and their managers. Usually, the most competent technician, the best qualified professional, is the most obvious candidate for promotion to the managerial role. Yet, research indicates that this background not only does not prepare the professional for management but may even equip him/her for failure. Most professionals' primary orientation is to their profession. I have known accountants leave their organisation rather than risk their professional standing through association or participation in what they consider to be questionable behaviour of their employer. Scientists who accept promotion to a managerial role experience the same conflict as they realise that their professional standing or current

is threatened by the additional demands and different behaviours imposed on them.

These generalisations need to be tempered according to the level of pragmatism shaping the perceptions of the individual. Thus, the engineer, as an applied scientist, has more in common with the manager with stronger pragmatic orientations and more similar career objectives. And indeed, as has already been indicated, we do find a high proportion of engineers embarking on managerial careers. Badawy suggests that the "management culture", that is, an amalgam of personality characteristics, management styles, value systems, type of position and management level involved is much more compatible, with the engineering culture than that of the scientist, particularly, the researcher.

As indicated at the outset, the purpose of this paper has been to set a basis for the subsequent discussions, to stimulate thought and to consider the management role in the context of the scientist/technologist. The problems of management for the technologist are quite different than for the typical manager, although similar to those faced by other professional groups. An understanding of these problems can be improved through an exploration of the educational experiences, the value systems, and role expectations of the manager and the scientist, and relating these to the role of the scientist manager (Table I).

It seems to me, in conclusion, that the consideration of these matters is of importance if we accept that effective management of technological functions is likely to be an emerging area of concern in line with the resource commitment which these functions are attracting.

INDUSTRY EXPECTATIONS OF SCIENCE AND PROBLEMS IN ITS MANAGEMENT

By BILL BRIGGS

Development Director, Chisholm Institute of Technology

Let me start by specifying the industries to which my comments are relevant and outlining the areas I intend to cover. The industries are the primary and secondary industries, and tertiary industries such as transport and communications which service the other two in the production of wealth. I am aware the economists would include other tertiary industries such as banking, retailing, tourism, entertainment, etc. but I see these as either facilitative of the basic "wealth producers" or of only secondary importance. I include scientific research and the generation of knowledge as wealth producing—if the results are exploited.

I shall treat science as "the systematic organisation of knowledge" and "scientific research" as the application of a particular intellectual process to the generation of new knowledge. It is important to draw the distinction between the scientist trained to generate and organise knowledge and the technologist (for example, the engineer) who is trained to apply knowledge to solve particular problems.

In looking at the expectations industry has of science I shall look at the situation within a particular industry or enterprise and at what industry can reasonably expect of the wider scientific community—including the university. I shall examine some of the problems encountered in making effective use of science, and suggest some solutions.

SCIENCE WITHIN AN INDUSTRY OR ENTERPRISE

Industry employs scientists because it needs their knowledge of a particular discipline, and their trained mind. It looks to science to solve its current problems and, in today's world, to create its new products and businesses. To make an effective contribution to meeting these needs the scientist must have the following attitude:

- imagination, creativity and an ability to spot opportunities;
- an appreciation of the methods of business and the constraints within which it operates;
- an ability to apply science to a wide range of problems; and,
- a knowledge of the process and the barriers to be overcome in bringing a new innovation from conception to profit making.

Time will not permit me to develop the methods of business and the constraints within which it operates in any detail but it is important we understand the essential features. They are:

- all business operates to satisfy a need;

- the enterprise operates in an environment in which it must compete or cease to exist;
- it must generate a satisfactory return on the assets employed; and,
- many constraints are imposed on it by government and by the community at large, e.g., the Trade Practice Acts, occupational health and safety regulations, product liability, etc.

The effective utilisation of science requires skilful and specialist management which must understand science and scientists and the process of translating new knowledge into profits. To use John Onto's definition, the role of that management is:

"Planning, organising, directing and controlling the activities of the scientist to achieve the desired goal of the enterprise."

The first and hardest task in managing science in an enterprise is to identify scientific goals which are consonant with and will support the overall goals of the enterprise. This may be relatively easy where a scientific team is engaged on process trouble shooting or product improvement but requires considerable vision, imagination, creativeness and an ability to persuade and convince sceptical colleagues or perhaps unimaginative bankers where the work may lead to new products or businesses or render an existing product line or business obsolete.

The second task of the manager of science is to create and maintain the environment in which the scientist can carry out this work. He must be free of the day-to-day distractions of business and have the resources needed for his task but also kept up to date within the goals of the enterprise, developments in the industry, company and government policies, etc.

Finally the manager has to monitor the progress of the scientist's work and make the hard decisions on when a project should be transferred from research to implementation, when it should be terminated or when a whole field of science or research should be abandoned. It is relatively easy to start a research project; it is far harder to kill it. To do so the research manager has to contend with not only the commitment and enthusiasm of the scientific team and their conviction that success is just around the corner, but also with the fact that he may have already spent large sums on the project which will be wasted if it is not successful, the worry that the scientists may be right and success is just around the corner, also with the problem that if he does abandon the work he may be left with people he can't employ elsewhere. Successful decision making in this area requires the early and careful definition of the problems to

be solved, the setting of progressive goals and the very careful monitoring of progress towards them. If the "problem gap" is not closing, alternative scientific strategies must be devised or the project abandoned.

It is also essential that the scientist and the manager constantly review the relevance of the project to the goals of the enterprise. Very often the manager must rely on the scientist to recognise and advise him of new developments which may make the project redundant, e.g., recognition of the significance of early publications on solid-state electronics made continued work on the vacuum tube irrelevant. Similarly the manager must also look to the market place—there may be no justification for continuing work on a project if the competition has reduced prices below a level at which the costs of further research and development could be recovered.

In employing scientists, industry also hopes that, at a later stage, the intellectual disciplines and training in problem solving which the scientist has received will allow him to make an important contribution to the management and later the direction of the enterprise. John Onto has offered us two hypotheses on the effectiveness of technologists in management. They are:

Hypothesis 1

That technologists are ill equipped by virtue of their training, values and other personality characteristics for the role of management.

Hypothesis 2

That the role of management, in the technological context, is in, and of itself, a precondition for failure in the job.

May I say that I support the first in full and stress than it applies even more strongly to the scientist than it does to the technologist or engineer. You will see I have reservations about the second. The scientist is trained to think divergently, to generate new ideas and new knowledge and not to accept constraints or convention; the technologist is trained to apply knowledge to the solution of defined problems. That training has already introduced him to some of the pragmatism needed in management. John Onto also referred to the significance of the differing personality traits, educational ex-

periences and value systems of the scientist and the manager and to Balderston's very useful analysis of their role differences which, if may I remind you, are shown in Table 1.

Whilst the scientist or technologist is trained (probably from the mid teens) to handle data and to solve well defined problems (and probably selected these areas because they felt more comfortable dealing with the concepts, quantifiable data, and defined problems of the maths, physics and chemistry than those with the human relations, communication skills and ill-defined problems encountered in the humanities), the problems encountered by the managers and directors of an enterprise are more often than not nebulous, ill-defined, unstructured and have no finite solution; skill in communication is often paramount. Thus the effective utilisation of scientists and technologists in management require not only the identification of those individuals who can make the transition to the management role but training in the skills involved.

The organisation must also ensure that the "Peter Principle" does not operate. That is, it must avoid promoting its best scientist to become an incompetent manager. As the hierarchy and reward structures of business are usually tied to the management structure the successful exploitation of science in industry must also offer a "career ladder" along which the scientist or technologist can progress and gain recognition. Whilst this can parallel the management ladder it is often difficult to cover the full range or to provide the same level of recognition available in the academic world. It can often be helpful to both industry and academia when a relatively free interchange of personnel between the sectors can be achieved.

INDUSTRIES EXPECTATIONS OF THE WIDER SCIENTIFIC COMMUNITY

Whilst industry expects to carry out the applied research needed for its development, it looks to the academic world and the wider research community for both the scientists trained to do that work and for the basic research needed for the generation of new knowledge, new enterprises and new sources of wealth.

TABLE 1
MANAGEMENT AND TECHNICAL SPECIALIST—SOME ROLE DIFFERENCES*

Management	Technical Specialist
Counsels, guides, directs people	Is consulted by people
Is sensitive to feelings, attitudes	Is intuitive, creative
Evaluates people's performance	Evaluates data systems or methods
Forecasts, analyses, controls costs	Technical performance outranks cost
High verbal skill required	High analytical skill required
Transmits and enforces policy	Logic outranks conformity
Directs what methods to use	Determines operational methods
Makes decisions from insufficient data	Seeks additional data
Accepts organisational hierarchy	Accepts hierarchy of truth
Seeks relationships to business goals	Seeks relationships among technical facts

Australia's tertiary education system has its roots in the British model and, I believe, that many of our academic research establishments were founded on the 19th century precepts of Oxford and Cambridge. Those precepts were that university research must seek knowledge solely for knowledge sake and that their researchers should be untrammelled by any association with trade or industry. It is worth remembering that the physical sciences were only recognised by Oxford and Cambridge many years after they were well established as disciplines in the German universities and at the Sorbonne and that in both Germany and France academia had, by then, established a close working relationship with industry.

A consequence of that attitude is that even today little attempt is made in English universities to protect intellectual property and that most of the new knowledge they generate is exploited elsewhere. The same has been the tradition and experience in Australia. The Oxbridge attitude is far removed from that at some U.S. universities—notably Stanford, Harvard and M.I.T. There the research scientist, whilst recognising that publication and the free communication of new knowledge is essential to the progress of science, seeks to protect the intellectual property therein and to exploit it for the benefit of their community and themselves. I believe that it is this difference in attitude which accounts for the so productive "science parks" in the Palo Alto, Silicon Valley and Cambridge areas of the U.S., and the absence of such developments in England. It also accounts for the international supremacy of the German chemical industry between say 1860 and 1945.

Whilst no one can question the success of Australian Universities in producing world class scientists and making a better than average contribution to the general growth of knowledge it is also true that only a small proportion of that work makes a direct contribution to the wealth of this nation. In today's highly competitive world in which basic research in other countries is either oriented to national goals, as in Japan and the eastern block, or serves communities with very large markets in which every strand of the work can be exploited through

their traditional close relationship between academia and industry (U.S. and Europe), Australia can no longer afford the luxury of its present policies under which some 80% of our research is solely for the pursuit of knowledge and is unlikely to make any contribution to Australia's wealth. It is, I think, a reasonable expectation of industry and of the community at large, which carries the cost of such work, that more of the basic research carried out in our universities be directed towards areas in which there is, at least, some reasonable, long-term prospect that the knowledge generated will be exploited by an Australian industry.

It is also reasonable to expect that the system should produce scientists who actively seek opportunities to exploit the knowledge they generate rather than being satisfied with the kudos they receive from publication. The U.S. experience suggests that these goals of pursuit of knowledge—free exchange and publication and exploiting the results are not incompatible and that the change in attitude required may be relatively small.

I have argued that industry employs scientists because it needs their knowledge and trained minds and that it looks to them to solve its current problems and to create new businesses and new wealth. I suggest that the nation's needs are the same and that the only difference is in the time scale. Similarly I suggest that the process and problems of managing science on a national scale are basically the same as those encountered in industry. Each requires:

- The identification of relevant goals;
- The provision of a climate in which science can flourish;
- The monitoring of progress towards those goals and the adjustment of the work program to achieve them; and,
- The courage to terminate projects which are no longer relevant.

Again the differences lie in the time scale and the magnitude of the task but also in that industry recognises the need for management and attempts to tackle the task—the nation does not.

SUMMARY

Let me attempt to summarise:

- An enterprise, an industry and the nation all need science to survive in today's competitive world.
- To be worthwhile science must be oriented towards goals which support the overall goals of the enterprise or the nation.
- Science must be well managed and directed if these goals are to be achieved and resources used effectively.
- Scientific training predisposes a person *against* effectiveness in management.
- Scientists can, however, be very good managers if the deficiencies of their training are recognised and they are properly selected and trained for the job.

Thank you ladies and gentlemen for your attention and the opportunity to express these perhaps iconoclastic views.

GOVERNMENT PERSPECTIVE—WHAT GOVERNMENT EXPECTS OF SCIENCE AND THE FUTURE ROLE OF SCIENCE

By K. FOLEY

Chairman, Australian Industrial Research and Development Incentives Board

I think that given the excellence of this morning's first session, especially the pertinence of the question period, it would be sensible of me to truncate the remarks that I originally intended to make, to leave as much time as possible for questions. I am able to do that to some extent because of remarks of both the Chairman and John Onto.

There is a great deal of overlap as you might have gathered from people like us on this particular subject, and I intend to talk briefly, hopefully not too briefly so that I miss raising a number of issues which will stimulate questions. I wonder, before I get to my paper, whether I should touch upon or at least provide my views, to give some sort of a background to my philosophy on the scientist/manager dilemma, and put my remarks in both a university and a Government science context.

I would certainly support the view, and I think it came from Philip Law, that once you get into those positions, be you a Vice-Chancellor or be you a Chief Executive, say from CSIRO, the criteria from which you are operating, the criteria on which you should be judged are managerial criteria, your managerial abilities, rather than your scientific abilities. I am looking with interest at what the Universities are doing with regard to their appointment of a Vice-Chancellor. I can quite easily foresee a situation whereby the Chief Executive, say of the CSIRO, or the Vice-Chancellor of the University is not a distinguished scientist and certainly does not practice in his field, whilst he is conducting duties of either the Vice-Chancellor or the Chief Executive of that organisation. It would seem to me that if I wanted a scientist in either of those organisations, I would be rather keen to see someone that was skilled in making sure that the maximum resources that could be obtained for my organisation were attracted to that organisation and they were used in the most effective way possible. I think it is unlikely that someone that is going to be reaching for that file relating to technical matters, all too often bulky, is going to deliver on that dimension, and I think one of the difficulties that one finds in the scientific community, both in the Government and outside is that we have not had a sufficient number of people in the Chief Executive position that are managers, that have had significant managerial skills, that have had their career in the managerial dimension rather than the scientific. Occasionally we find that happy co-incidence where you have an excellent scientist, a person distinguished internationally very often, who can move into a managerial role and perform that excellently and

still stay up with his discipline. I would say that that is something of a rarity and one shouldn't be organising situations for that almost unique person.

If I could come now to my topic and by way of a caveat, say that obviously, I cannot give a Government view on science and management. The Minister to whom I report as Chairman of the Industrial Research and Development Board may well be horrified if he thought I was doing that. What I can do and will, is to give the benefit, for what it is worth, of the view from someone that has worked now for almost exactly a year, a year this week in fact, in the Government scientific community; or at least close to the Government scientific community as Chairman of that Board reporting to the Minister for Science and Technology and therefore operating to some extent in that wider Government context of his portfolio; but also very importantly being given the opportunity to relate to the wider scientific community, that is, those scientists that reside in Government, in that quasi-Government area as well as in the universities, and more particularly perhaps, but certainly not exclusively in industry. So I would like to draw on that experience to provide a perspective on the manager and science.

When Bob Taylor asked me to address myself to this topic it struck me that there were two issues that needed to be addressed. They are not mutually exclusive, but I think you can address them to some extent, separately. The first one is the management of science in Government itself, and then the topic that we have been tending to talk most about this morning and that is the management in science. If I can come to a quick summary and then come back to elaborate later on, I would suggest to you that the quality or the level of management in both of those areas is excessively low and that we all suffer significantly as a result of that.

I think it is sensible, not for perhaps a couple of you in this room, but most of you whom I am not familiar with and with whom I have had no contact in the last year, that I make some brief mention about the Industrial Research and Development Board, so that you can understand the platform from which I am generating these views. So I would like to do that, with apologies to a couple of you, for just a few moments before I go on to talk about the management of science by Government, or how Government manages the scarce resources that it provides to Science, and the increasing resources that it is providing to science; secondly coming back to looking at the level of the quality of management in science. The Industrial Research and

Development Board has been in operation since 1976. There has been a scheme much the same as the scheme that is operating now, since 1967. The basis for the scheme, the Board, is to encourage research and development and transfer the benefits of that research and development to the Australian community. It is currently funded in excess of \$70 million, so that it provides a significant infusion of funds into the scientific community, perhaps with a couple of very minor exceptions, which I won't go into. It is important for me to point out that those funds go right across the scientific community and we indeed are the only organisation within Barry Jones' portfolio, and possibly in the Federal Government as a whole, that goes right across the scientific spectrum, as I said with possibly a couple of minor aberrations which we are currently trying to correct. Whilst there are a number of components in the scheme, which I won't elaborate on, some two-thirds of the funds go to encouraging research and development and the benefaction of that research and development, through research and development/design projects, so members of the scientific community, whether they be in industry or whether they be in universities or in other research institutes (if they believe that they have a project which they would otherwise not go ahead with, is too expensive, or too risky, or they would not otherwise go ahead with at the appropriate pace), can present that project to the Board, which is a 12 person Board, with members again from across industry and the scientific community, not quite yet from across the country, but with the major States being represented.

The remarks I make about the quality of management will really relate to the material that one sees in the organisations that one visits in pursuit of evaluation of a particular project. Perhaps it is important just to give you a slightly better feel for the organisation to see that the annual limit for funding is \$750,000 and they are still talking about those projects. They are funded by and large on a dollar for dollar basis so one is talking about some fairly large projects, that is, about a million and a half dollar project at the top end, and the average is a little less than half that. So we deal with some very, very significant sums of money and to come back to a point that the Chairman was touching on this morning, it is therefore an organisation that most people in this room should know how to interface, and I would suggest to you that most people in this room do not know sufficient about it (which is partly your problem and partly mine but certainly not entirely mine or the Government's), wouldn't know how to effectively interface with it, and as a result of a deficiency in presentation that relates to a large extent to the capacity to manage multi-dimensional and multi-disciplinary projects, perhaps wouldn't be able to be successful in an application before the Board.

Let me now turn to talking about the first issue, and that is the management of science by Government. There are a number of you in this room that have heard me talk about this on a number of other occasions and I put it to you that as I complete my first year in this job, which I should also remind you is only part-time, my

greatest concern relates to this point. It isn't my greatest concern that there is not sufficient managerial skills in the scientific community. My greatest concern comes from my observation that there is very, very little focus on the management of scarce resources of the Government which applies to the scientific community. In the industrial domain, particularly, which is the one that we have to concentrate on to a large extent, there is a plethora of organisations which fund the scientific community. They are unco-ordinated, there is little or no co-operation between them. There is no co-ordination and they are not embedded in a policy, in a science policy if you like, in a very broad sense and certainly not embedded in an industrial research and development policy at the more narrow level. So the level of management which is applied to this rather large amount of money is very, very small indeed. In fact, one can say that the whole scheme of things is administered rather than being managed. Perhaps here I should pause and indicate a prejudice that will run through most of my comments, and has been running through my comments as you will have observed thus far. The perspective that I have on the world is a managerial perspective, not an administrative perspective and I will make the comment by way of conclusion I think, that the perspective that has been brought by the scientific community itself and by Government to this domain, has been administrative rather than managerial. But more of that later. I won't elaborate on the difficulties and what I regard as the deficiencies that stem from this lack of co-operation and co-ordination and coherence and so forth in the management of science by Government, but I am happy to explore that in as much detail as you would want through questions.

Let me turn now quickly to the second point, management in science and let me do that by talking about my activities on the Board. In the course of a month, I had cause to evaluate privately, and then later in the company of my Board colleagues, with assistance from no doubt very many of you in this room, as referees, some 50-60 quite significant projects relating to research and development, all of them put together by people from the community that we in this room represent. In the course of that month, I would also visit some 10 or 15 firms and speak with members of their research departments, if I am talking about private enterprise, or I would visit a university where, if the university is being far-sighted, I would be able to talk to a research institute that specifically focuses on industry and has a fairly acute understanding of organisations like my own. In some universities that is not possible. They do not organise themselves in such a way that they have concentrated resources that will focus on industry and will focus on Government. It's done on an ad hoc Department by Department, scientist by scientist basis. So, I will go to universities and CSIRO or research institutes and in the course of that go through two situations.

Firstly, one of euphoria when one sees people and the ideas, and the products in many cases, that abound

in this country. It really is quite extraordinary and one looks at it and can't believe that the future would be anything other than rosy for this country. There are some extraordinarily talented people in the Australian scientific community. That is the euphoric phase, seeing what the ideas are and what the capacities are in the scientific community, and as I say in many cases, actually seeing the product. The let down comes shortly afterwards when you realise that the idea or that prototype, if you like, or that rudimentary product or the project that relates to all that has to be managed, has to be brought together and people have to operate to a budget, to some sort of planning horizon and so forth. The let down starts when you see otherwise quite fantastic products that are really just not going to go anywhere given the way they are put together and the way that they are described and the way they are "managed". Very often they are managed by a chief scientist, the person that has generated the idea, and his commitment is to the technicalities of the issue rather than managing the entire operation and he will perhaps, very reluctantly, drag himself away from the microscope or whatever it is that he is looking at, to worry about development of funds, marrying together this rather difficult group of people that often speak a different language, that come from different disciplines. I can't recall a project yet that is not multi-dimensional or multi-disciplinary and requires some rather special skills, some managerial skills to bring it all together. So you see these otherwise excellent projects, products, ideas, either not going anywhere, not capable of going anywhere given the way they are structured or which will stagger on perhaps and achieve some 10 or 15 or 20 per cent of their real potential. That in itself is bad enough but the vast majority of products that we look at have to be marketed, not sold, but marketed. There is a pretty fundamental distinction between those two concepts; a distinction that many people in Australian industry have not come to grips with. But when you come to realise that the community will only benefit by those funds being put into the market place and more particularly in many cases going to the international market place, and you look at the marketing skills that are present or proposed to be present, or purported to be present, in those projects, one is really almost totally let down because even if the thing looks as though it is being managed properly, if you can't put it into the market place then you might as well have stayed at home. You will probably have achieved an excellent piece of research and built a rather interesting prototype, probably generated a couple of scientific papers out of it but really in terms of contribution to society you have achieved near enough to nothing and you have achieved that because two components of the exercise have been neglected. You can shrink them into one and talk about management and let's assume that embraces marketing, or you come back into the two as I like to, but the marketing and the managerial side have by and large been neglected. There are very many of us who really don't want to get involved in that anyway. We are much more interested in the scientific aspects of what we

are doing but given that the vast majority of funds come from Government research funds, funds that go into the scientific community come from Government and the community. If you really want to sustain your position, and the scientific community is not sustaining its position at the moment, then you have got to, at some stage, convince the community that you can provide them with some benefit as a result of those funds they are expending. I don't think they are expecting that every cent that is spent will produce some exciting product but they are expecting to see some nexus and in very many cases, I think, they do not, which perhaps partly explains why the funds to the scientific community, and most disturbingly the funds to basic research, have shrunk so much.

I discovered the other day that someone was saying to me "well we will just have to start lobbying and get some more funds into pure research" and someone said "well really by lobbying you are not going to get a quantum leap forward, you are only going to make a marginal adjustment" and someone said "well that is probably all that we should be hoping for" but then into the discussion it was intruded the fact that in real terms funds to basic research in the last, I think, 15 years have declined by 40%. So if we want to get back, and they were hardly the healthiest days, if you want to get back to something even approaching that, then you have got to be finding ways that will have you, rather than pecking on the periphery, causing Government and others who contribute funds to make some great leaps forward.

So to try and summarise, there is this quite incredible chasm in this country and it is quite unique in the industrial world. A chasm as deep, as black, as great in this country between what we produce as a scientist by way of research and often up to prototype product stage and what we actually put in the market place. There is no country in the world that does anywhere near as badly as we do. The base from which we operate in this country, as Barry Jones is so often saying, is as good as the base of any other industrial country in the world. It is excellent. The research skills in the country are extraordinary but it's those other steps along the way that we fall down on. One of those steps, or one of those disciplines, one of the sets of skills that is required to allow us to get a better return on that quite remarkable talent is management. It is one that has intruded itself to a very, very limited degree into the scientific community really. But it is, in my view anyway, from that community and our ability to capitalise on what happens in it, that we will derive our future. And, as I say, because we are not doing too well at the management at both the Government level and the scientific community level we are unlikely to get anywhere near the future that we could achieve if we operated ourselves slightly differently.

Mr. Chairman I have spoken longer than I wanted to. Let me just touch on four points which I would like to make by way of summary. The first one is that Government has no coherent policy on the application of science to community benefit and that is certainly true

and I would underscore that. I would also underscore for the present, that this Government is turning its mind to this matter in the industrial area, in the industrial application of science. The second summary point that I would make is that management is not, and I would emphasise not, seen by the scientific community or that part of industry that is involved in science, as a separate and distinct skill. I would argue very strenuously that it is and that it takes just as long to come, and to come to a point that John Onto was making this morning, it requires just as much rigour; you do it in a very different way, it takes just as long to acquire, it's just as hard to acquire the skills of management as it is to acquire the skills of any other discipline that I know of. Most of us tend to think if you are good at something else, whatever something else may be, be it an airline pilot or a scientist of any description, then automatically at some stage of your career you can become a good manager. I would suggest to you that is far from the truth. The third point, indeed it is the last summary point that I have written down, is that both Government and the scientific community have been content to administer its resources, which come largely from a process of what I described as disjointed incrementalism, rather than assist in the development of science policy and manage its scarce resources. I haven't elaborated on what I see as the difference between management and administration but I am happy to do that later. So my final point would be this, that unless the scientific community adopts that managerial/policy perspective, gets itself involved with Government and indeed with industry at their policy setting, objective setting level, then the scientific community is doomed to be playing on the periphery, being described as "whimps", as Barry Jones is wont to

describe the scientific community, from time to time, and working to wholly inappropriate, very, very frustrating, short and discrete planning horizons. Almost everyone here is in the business of working in a context where the planning horizons are exceedingly long and you need a continuity to be effective within it. If the context within which the Government forces you to work (and there are other contexts I know, but I am talking about the largest and most significant sources of funds) is disjointed, it's discrete and it's incremental, there is, I suggest, a contradiction in those terms.

I suppose the science budget is not much different from most other budgets, and the one that springs to mind is the defence budget which I often argue the current defence budget was possibly set back in the 1940s and all we have been doing with it ever since is making whatever incremental adjustments people could argue, usually in terms of some particular hardware and usually in terms of the replacement of a particular piece of hardware, and not in terms of what it can achieve for the community. So, the science budget has tended to be that way too and what I am arguing is that it will continue to be that way unless the scientific community can intrude itself into the process in a very different way, and that very different way will come from having a management perspective, if you like, on the whole scientific endeavour rather than a narrow, partial and even an ad hoc one. So, what I have finished up saying is that if you are in an environment where the planning horizons are short and discrete and the budgets tend to be established through a mechanism that I have described as disjointed incrementalism, and such a situation presently exists, it isn't in the interests of anyone that it should continue.

Mr. Chairman, thank you very much.

THE MANAGEMENT OF SCIENCE—FUTURE DIRECTIONS AND CHALLENGES. COMMUNITY PERSPECTIVE

By R. H. TAYLOR

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Perceptions are very much in the eye of the perceiver and are difficult to quantify. However, it is possible to trace significant changes in community perceptions if one looks back over the period between Hiroshima and Sputnik to the present. To illustrate these changes I have chosen to discuss one small area of science—the use of pesticides—which I believe reflects much of the changing community perceptions to science over this period.

In the 1950s, scientists involved in chemical control of pests and diseases were presented with a large array of extremely effective chemicals as judged by the criterion of rapid destruction of living organisms. Such scientists were seen as positive and productive members of society and fitted the traditional heroic image of scientists which had prevailed for the previous century. By the 1960s, Rachel Carson and others had blown the whistle on DDT but scientists in general failed to perceive the winds of change. They were preoccupied with the development of resistance by target organisms to pesticides but were not paying adequate attention to the growing environmental concern of the community, which incidentally included some of their more perceptive colleagues. In the 1970s, after the turbulent 1960s and in particular the use of crude 245 T in Vietnam, scientists began to realise that, like Vietnam veterans, they were returning from their campaigns as anti-heroes. Even in this climate, scientists persisted with their traditional logical and analytical defence. They argued that if such chemicals as 245 T were used with care, many tests and enquiries have proved them to be safe.

Scientists were bewildered to find that an increasing sector of the public did not accept their logic. Politicians whose jobs depend on judgements of public perception reflected the public disquiet and were much quicker to detect the fears of the public than scientists and they were influenced by a press that was quick to detect what interested the public. The politicians, because of this issue and others, began to query the credibility of scientists. So, scientists have arrived in the 1980s with a belated understanding that they must be accountable for their technologies in a very broad sociological and economic context. It is not that scientists had not heard, but rather that they have regarded their science as being of such value that social issues would somehow sort themselves out to adjust to technological advance.

The question we must now address with urgency is, how can scientists play their part in the introduction of technology in a manner which is acceptable to a community who on one hand embraces it and the other, fears it. The responsibility rests squarely on the managers of scientists who must be prepared to spend time in communication, education and negotiation—skills which are not part of their scientific training and which during the early working years appear to be unproductive and unlikely to bring status or reward. It is now not good enough for scientists to move to management for higher rewards or status with the naive belief that management is common sense and that anyone who thinks analytically and logically will soon encompass it as a vocation.

AN ACADEMIC'S PERCEPTION OF THE INTERACTION OF UNIVERSITIES WITH THOSE WHO "MANAGE" (OR WOULD LIKE TO MANAGE) SCIENTIFIC ACTIVITIES

By NANCY F. MILLIS

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THE PRIME RESPONSIBILITIES OF UNIVERSITIES

1. *Hand on the state of the art*

- 1.1 Basis laws and fundamental knowledge.
- 1.2 Expose young scientists to the way in which the scientific method, and experimentation lead to hypotheses and an appreciation that an hypothesis must be testable if it is to be useful.

2. *Advance knowledge*

- 2.1 Probe unknown or poorly understood areas—develop new hypotheses; curiosity driven research. To uncover basic principles but to be alert to potential applications.
- 2.2 Train scientists in this kind of research—stimulate, encourage novel ideas in young postgraduates.

Because of the long term nature of pay-offs from that work—it is *government* which will pay for this work—it is a national investment. The prime responsibility of universities is to produce graduates who have independence of thought, a heightened imagination, and the technical competence to pursue ideas and to pursue excellence in research, be it fundamental or less fundamental. BUT, there are other responsibilities, some relating quite closely to the management of science.

3. *Dissemination of knowledge/influence in the community*

- 3.1 Professional societies—raising awareness of new ideas by presenting papers at conferences, and offering courses to up-date members learning about current problems which arise among practitioners, learning about the needs of professionals.
- 3.2 Providing disinterested but informed advice to government on enquiries, standing committees, refereeing grant requests (ARGS, NHMRC), policy decisions (serve on agencies/regulatory agencies/boards). Review the scientific activities of governmental agencies.
- 3.3 Public affairs, e.g. ABC, Hospital boards, NATA, National Standards.

Having stated how I see universities as managing science within their own sphere and in the rather wider public arena, does this leave a place for them to interact with industry?

4. *Contact with industry*

- 4.1 Universities must remain free to offer the instruction and pursue the research they believe will best advance the science in their particular discipline.

Industry has a right to expect a thinking competent scientist, but they cannot expect scientists trained specifically for their needs. Notwithstanding that view, I do believe it is possible to find many research projects which are of mutual interest to university and industry. Here the benefits flow directly to industry and industry needs to be more prepared to pay than seems to have been the case in the past. Industry/university interactions can take the form of:

- 4.2 Consultancies with industry.
- 4.3 Joint research projects in the forms of: Funds from industry (contract research), research at university; Staff from industry, research at university; Staff from university, research in industry; Purchase of time and skills on expensive equipment; Problem solving with industry ad hoc and associated with innovation.

What criteria make such work appropriate for a university? It may be undertaken because:

- (a) it has a significant element of investigation (along with more routine aspects);
- (b) the work funds the purchase of a facility which enables the Department as a whole to benefit, although the work itself may not be highly fundamental;
- (c) it provides flexible funds to a research group in return for sharing the rights with the industry to exploit the application of any research findings sponsored by industry;
- (d) by providing funds from routine analysis (for example), a Department may be able to employ a technical assistant or buy a better piece of equipment; and,
- (e) it allows university and industry to share in the application of research findings.

I believe the benefits from such associations are significant.

Certainly academics can do with an increased awareness of industrial activities. Academics should be aware of the following about industry:

- (a) what it would like to do;
- (b) what it is doing less well than is possible with the application of current knowledge;
- (c) what it might do with ideas, if it (industry) knew they existed; and,
- (d) where industry is experiencing problems.

The lack of awareness by industry of the expertise in universities and CAEs is also a real concern, especially in industries where either they don't have a Research and Development Department at all, or it is very small.

RECENT CHANGES ON THE SOMERS-SANDY POINT COASTLINE, WESTERNPORT BAY, VICTORIA

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ABSTRACT: The sandy foreland east of Somers, culminating in Sandy Point, consists of numerous sub-parallel dune ridges, the pattern of which indicates long-term accretion of sand supplied from the sea floor to the south-west, and a predominance of eastward drifting by waves and currents. Recent stages in the growth and evolution of the southern coastline of this foreland have been traced from successive air photographs, and during the past decade repeated surveys on 24 transects have demonstrated continuing erosion, and eastward drifting to accreting sectors at Cormorant Point and Sandy Point. Estimates of areal and volumetric losses and gains are presented: they show a net loss from the beach system, some of the sand being carried on to backshore dunes and some being removed offshore to the extensive bar system that runs out to Middle Bank.

In the south-west of Westernport Bay (Fig. 1) the coastline between Flinders and Somers consists of bluffs and cliffed headlands fronted by shore platforms, all cut in weathered Tertiary basalt. Sandy beaches, backed by low grassy dunes, occupy successive embayments, narrowing as they pass the rocky headlands. At Balnarring, scrub-covered dunes behind the beach are backed by the channel of Merrieks Creek, which runs eastwards to enter the sea in the lee of a group of rocky reefs exposed at low tide. At Somers, to the east, the sandy beach and backing dunes run behind a broad shore platform, and are backed in turn by steep bluffs. East of Somers the bluffs curve inland and the shore platform comes to an end, but the sandy beach continues, backed by extensive dune topography, for another 5 km to Sandy Point. Off this point, sand bars and shoals, partly exposed at low tide, run out south-west to Middle Bank, and between these and the sandy beach seagrass beds are extensive in coastal waters.

The Somers-Sandy Point beach system (Fig. 2) forms the southern flank of a large sandy depositional foreland, bearing numerous sub-parallel dune ridges (Jenkin 1962). The beach, 50 to 70 m wide at low spring tides, consists mainly of fine to medium quartzose sand, with some coarser material, including pebbles of calcareous sandstone similar to the dune calcarenites which occur along the Victorian coastline at several locations, notably the Nepean Peninsula at the entrance to Port Phillip Bay to the west. There are also a few pebbles of basalt, derived from erosion of the shore platform at Somers. Parts of this beach have recently been cut back by marine erosion, and the dunes to the rear are cliffed (Fig. 3), but others have been built up by sand accretion, and are backed by low, grassy dunes (Fig. 4).

Historical changes on this coastline have been documented with references to maps, charts, air photographs and ground photographs (Figures 5 and 6) of various dates, supplemented during the past decade by repeated surveys of the beach. Before considering these, it is

necessary to describe the processes at work on the shore and in the nearshore zone along the Somers-Sandy Point beach.

PROCESSES

Mean spring tide range on the coast between Balnarring and Sandy Point is about 2.5 m, increasing to just over 3 m at maximum spring tides and diminishing to about 2 m at neap tides. High tide arrives at Balnarring Pier 5 to 15 min after Flinders, and reaches Sandy Point another 5 to 10 min later.

As the tide rises an eastward current develops off the coast between Point Leo and Balnarring, moving inshore along the Somers-Sandy Point beach. The relationship between mean spring tide and nearshore currents east of Somers on a windless day is shown in Fig. 7. Maximum current velocity occurs about 1.5 hr after mid-tide. Flow velocities of up to 80 cm.sec.⁻¹ (about 1.6 knots) have been recorded here on calm days at maximum tides.

As the tide ebbs a strong outflow develops off Sandy Point, splaying out south-westwards over Middle Bank (Fig. 1), but inshore there is only a weak westward ebb towards Somers, rarely attaining 25 cm.sec.⁻¹.

Ocean swell enters Westernport Bay between Flinders and Phillip Island from a southerly direction, but is much weakened as it passes through the shallow water. Refracted ocean swell (wave periods typically 8 to 14 sec) frequently reaches the shore between Point Leo and Balnarring, and has shaped beaches with gently-curved 'swash alignments' (Davies 1972). East of Balnarring these swell waves diminish because of the sheltering effect of Middle Bank. They can sometimes be detected on the shore between Somers and Sandy Point at high tide, particularly when they are reinforced by strong southerly winds, but as the tide falls the ocean waves break heavily on Middle Bank, and at low tide they do not penetrate the nearshore waters.

Wave action is also generated by local winds, which produce short period (3 to 6 sec) waves, arriving mainly

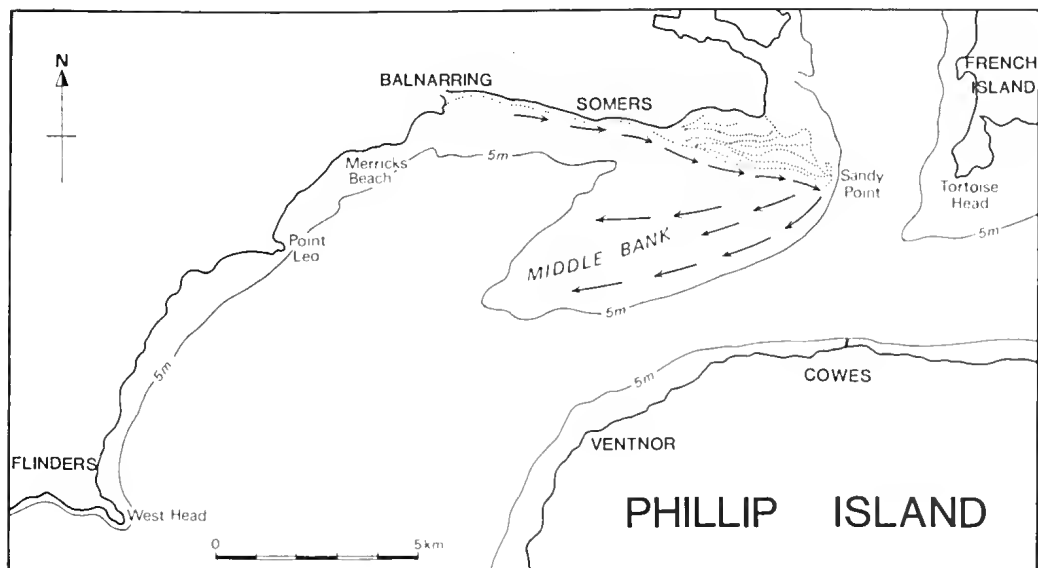


Fig. 1—Coastal features in the south-west of Westernport Bay, showing the location and outline of Sandy Point. Arrows indicate the predominant eastward longshore drifting (resulting from the approach of south-westerly waves and a strong flow current inshore as the tide rises) to Sandy Point, and the movement of sand from there (dispersed by ebb currents as the tide falls) to Middle Bank.

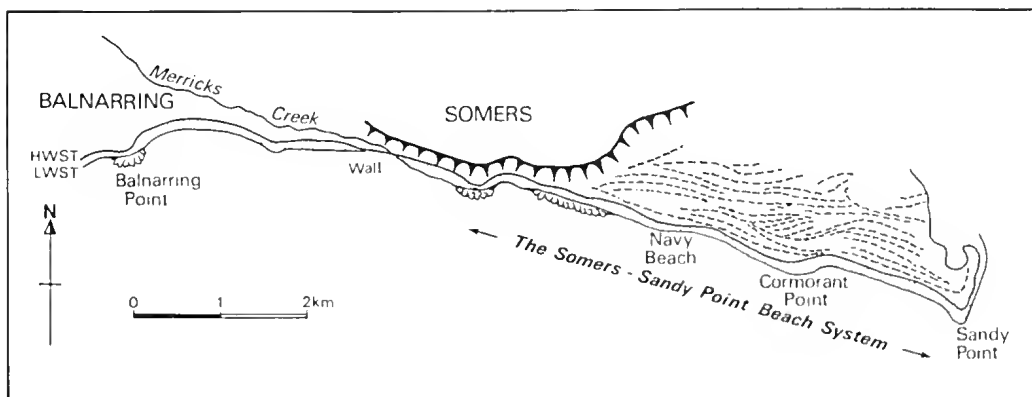


Fig. 2—The Somers-Sandy Point beach system in relation to the bluffs and shore platforms cut in Tertiary basalt at Somers, and the sandy depositional foreland, on which dotted lines indicate predominant trends of foredunes.



Fig. 3—Retreating sector of coastline east of Somers in October 1969. Erosion at the base of the dune cliff by storm waves at high tide has undercut tea-tree (*Leptospermum laevigatum*) woodland. Photo: Eric Bird.



Fig. 4—Advancing sector of coastline east of Cormorant Point, looking towards Sandy Point, 7 December 1984. Behind the driftwood zone on the right are sand hummocks developing under *Cakile maritima*, and in the foreground the sand has been colonised by marram grass (*Ammophila arenaria*). Photo: Eric Bird.



Fig. 5—A view of the coastline east of Somers, taken by J.T. Jutson on 10 December 1933. A note on the back of the photograph describes it as "just about where the basalt country falls away and gives place to a peninsula of blown sand". Fig. 6 shows the same sector as it appeared in December 1979. Photo: Geological Survey of Victoria.

from the south-western quadrant, but occasionally from the south-east, notably when an anticyclone is moving into this region from the south-west. At Balnarring the waves coming from the south-west are small, because of the short fetch and the sheltering effect of the hilly hinterland of the Mornington Peninsula, but farther east they increase in relative height and, arriving obliquely, produce an eastward beach drifting. The same waves generate a longshore current eastward to Sandy Point, which augments the tidal flow current, but opposes the weaker inshore ebb. It is difficult to measure longshore currents when strong south-westerly waves accompany a rising tide because of the pulsations of wave action, but it is likely that east of Somers they exceed 1.0 m.sec^{-1} . At low tide, wave action is diminished because the nearshore waters are relatively shallow, and the dense seagrass communities absorb much of the wave energy.

The prevailing winds are from the west, and these also contribute to the predominance of eastward drifting of sand between Somers and Sandy Point, especially when they blow strongly, and carry dry beach sand alongshore: the process is similar to that described from Portsea Beach by So (1982). Occasional south-easterly winds may temporarily reverse this aeolian drifting.

In contrast with the beaches south-west of Balnarring, the Somers-Sandy Point coastline has a 'drift alignment' (Davies 1972). Eastward drifting has deflected the mouth of Merricks Creek towards Somers, and a succession of lobate sandy forelands has formed, and migrated along the shore towards Sandy Point. In the nearshore zone near Sandy Point Marsden, Mallett and Donaldson (1979) noted large sand bars at right-angles to the coastline, driven eastward by the rising tide. Farther offshore, the bars and shoals that run out south-west from Sandy Point to Middle Bank consist of sand deposited by ebb currents. The underwater topography has been shaped partly by ocean waves breaking on the southern margin of Middle Bank, and partly by interacting waves and currents in nearshore waters as the tides rise and fall. The seagrass beds extensive to the west of these bars and shoals, dominated by *Zostera* spp. and *Amphibolis* sp., are quiet environments within which fine to very fine sand and silt have been deposited. Sand bars migrating eastwards inshore bury and destroy seagrass vegetation, but it revives after they move on. Observations of sand bar migration during the past decade here showed little evidence of shoreward movement, except briefly during occasional periods of south-easterly wave action, when



Fig. 6—The coastline east of Somers, as it appeared on 19 December 1979, with Ports & Harbors' Pole No. 15 in the foreground, and No. 16 in the middle distance. The wooden wall on the left was completed in 1978. Compare Fig. 5.

some sand from the bars off Sandy Point has been delivered to the beach. While it is possible that sand swept out to Middle Bank by ebb currents could eventually find its way back on to the Somers-Sandy Point beach, this has not been happening in recent years.

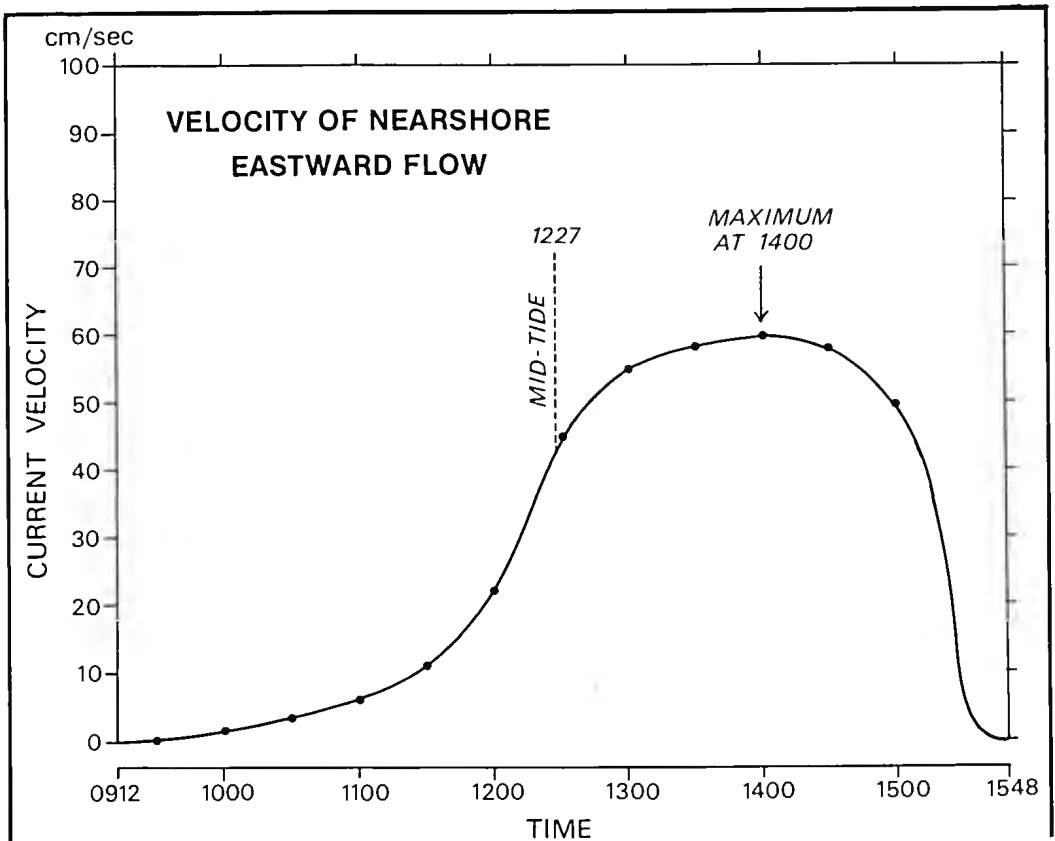
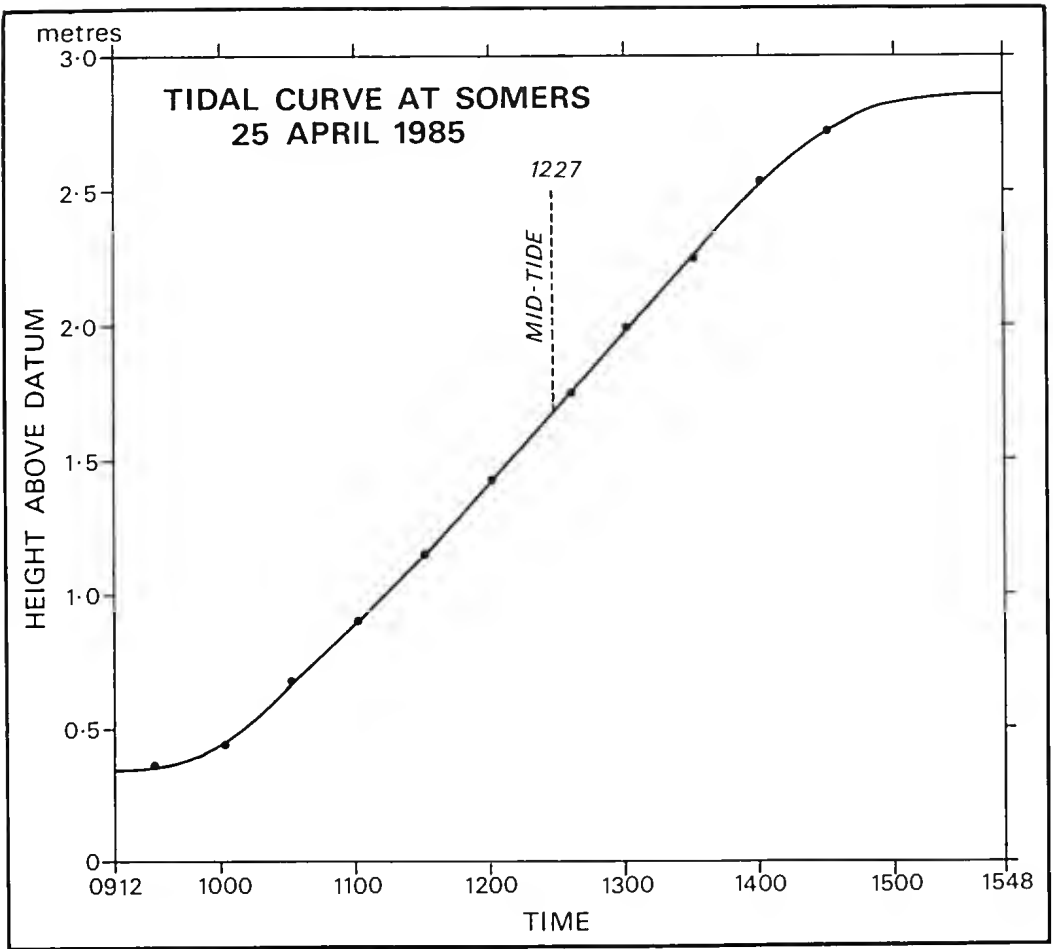
THE SANDY FORELAND

The pattern of dune ridges on the sandy foreland east of Somers is visible on air photographs (Fig. 10), and has been mapped by Jenkin (1962). The area is Commonwealth Land, under the control of the Royal Australian Navy Flinders Depot (H.M.A.S. *Cerberus*). It was first described by the French explorer Dumont D'Urville (1833), who landed on Sandy Point during a visit to Westernport Bay in the *Astrolabe* in November 1826, and walked inland across parallel ridges and swales so regular that he found it difficult to believe they were not man-made. The ridges have an amplitude of up to 3 m, and soil profiles beneath the ridge crests increase in depth landwards, indicating that they formed successively on a prograding sandy coast. The oldest (i.e. innermost) carry *Eucalyptus* woodland with an understorey of bracken and some heath plants. This gives place seaward to *Banksia integrifolia* woodland, then *Leptospermum laevigatum* (coast tea-tree)

woodland, declining to scrub and grassy vegetation on the youngest dunes, immediately behind the beach. The soil profiles and vegetation associations are similar to those described from the sand ridges of the outer barrier in East Gippsland, behind the Ninety Mile Beach (Bird 1978), and are considered to be of Holocene age, but it is possible that there is older (i.e. Pleistocene) sandy terrain farther inland.

The sandy foreland has thus been deposited in the period since the Holocene marine transgression brought the sea up to approximately its present level about 6,000 years ago, establishing the general outlines of Westernport Bay (Marsden & Mallett 1975). At this stage the coastline east of Somers consisted of cliffs behind shore platforms cut in Tertiary basalt, but soon the deposition of sand began.

The sand is quartzose, with associated calcareous material. It cannot have come from the Tertiary basalts, which weather subaerially into clay, and are eroded on cliffs and shore platforms into cobbles, pebbles, and a little sand, added to nearby beaches. This sand is black, and mineralogically distinct from the beach and dune sands east of Somers. In the absence of a local fluvial sand supply (Merricks Creek delivers only small quantities of silt and clay) the sand must have come



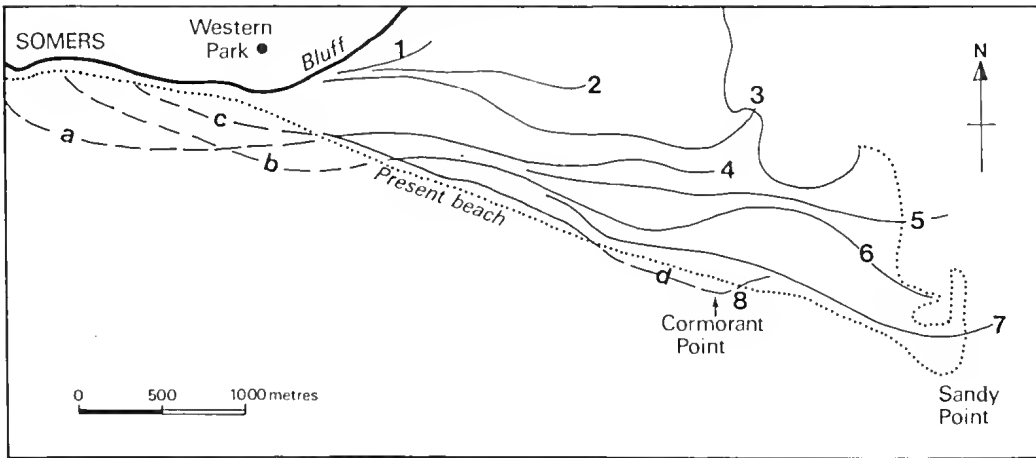


Fig. 8—Stages (1 to 8) in the evolution of the sandy foreland east of Somers, deduced from selected dune ridge alignments. For explanation see text. The dotted line indicates the present configuration.



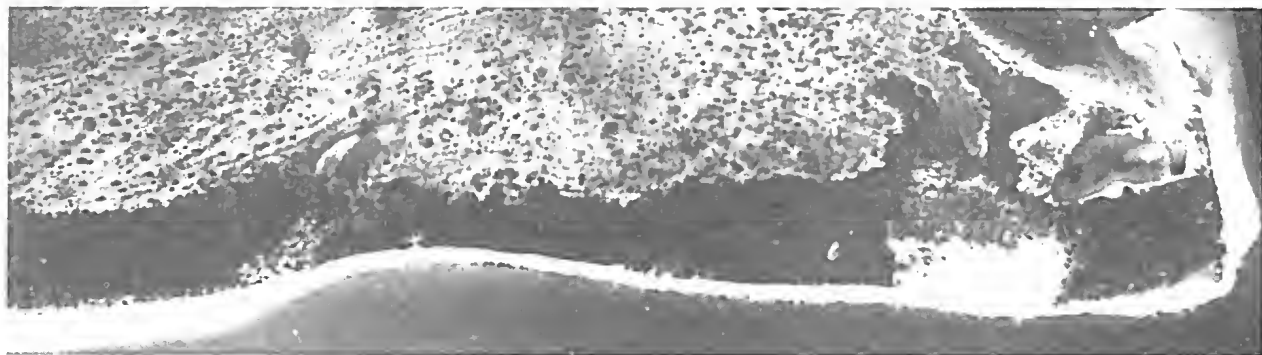
Fig. 9—A view west from Sandy Point towards Cormorant Point, showing the relict (1939) coastline on the right, and a foredune, initiated on a wave-built beach ridge in 1974 and subsequently built up by the trapping of wind-blown sand in marram grass (*Ammophila arenaria*), separated from the earlier coastline by an unvegetated swale. Photo: Eric Bird.

from the sea floor to the south and south-west. It is deduced that, as the Holocene marine transgression came to an end, sand shoals formed in the sea area between Flinders and Phillip Island, and were carried shoreward by wave action to be deposited as beaches along the bordering coasts. Much of the sand delivered to the coastline between Balnarring and Somers has drifted eastwards to be incorporated in the sandy foreland. It is possible that progradation here was assisted by a slight emergence following an episode of sea level 1 to 2 m higher than at present as the marine transgression came to an end, for there is evidence for such an episode at several places around Westernport Bay (Marsden & Mallett 1975).

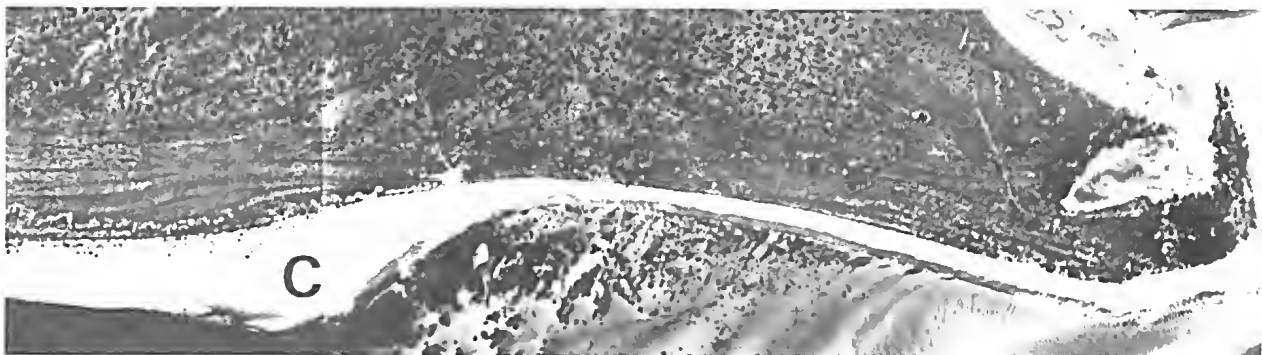
The numerous sub-parallel ridges are evidently relict foredunes, each formed in the zone behind a prograding sandy beach, and each commemorating an earlier position of the coastline. The various ways in which such foredunes are initiated has been the subject of recent discussion (Hesp 1984, Bird 1985a), but it is generally agreed that they indicate stages in an evolving coastal configuration.

Stages in the growth of this sandy foreland may be deciphered from the dune ridge pattern (Fig. 8). At stage 1, a beach formed in front of the bluff at Western Park, and at stage 2, a ridge developed in front of this, and extended further eastwards: the intervening hollow is occupied by a swamp. With further sand accretion,

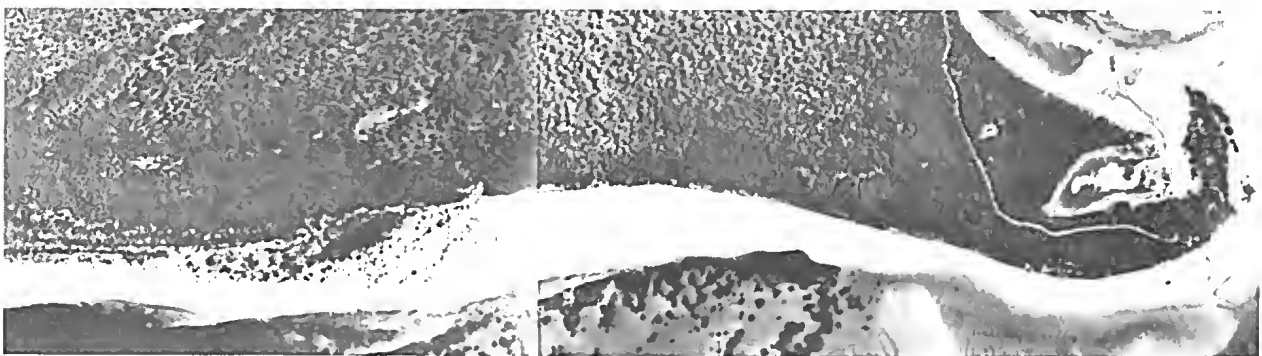
Fig. 7—Measurements of the rising tide and nearshore eastward current flow measured 10 metres offshore at Pole 21, east of Somers (see Fig. 14).



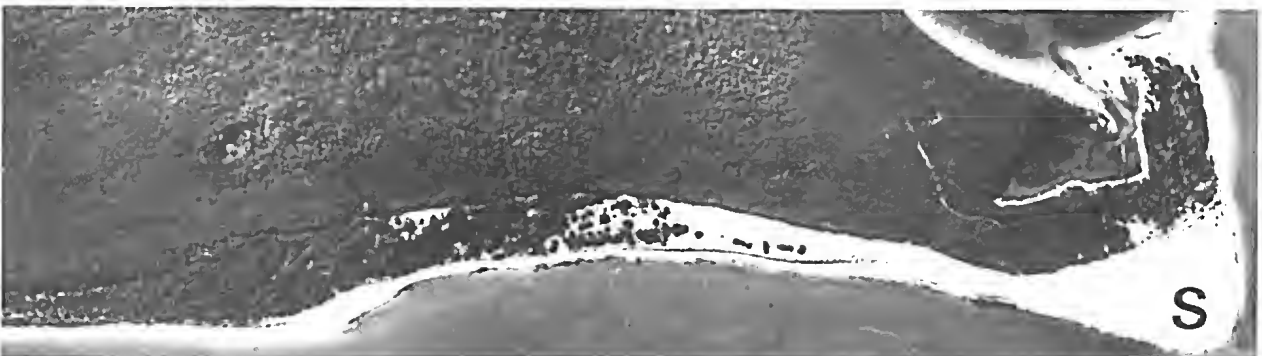
1 April 1939



3 April 1956



16 January 1968



0 1000 metres

18 May 1984

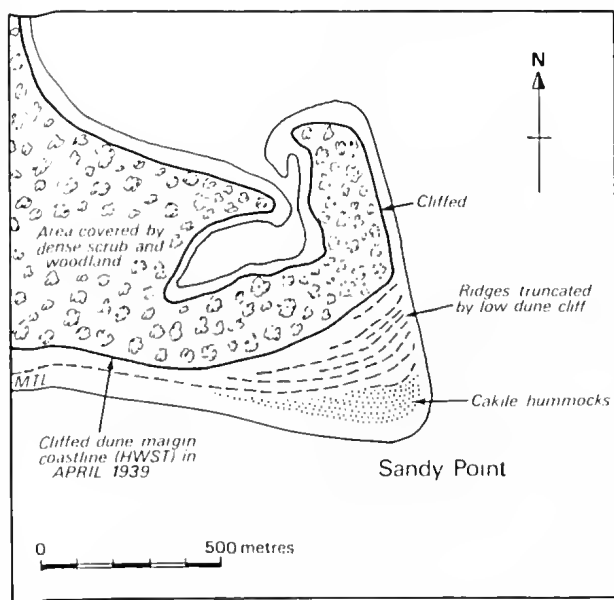


Fig. 11—The outline of Sandy Point (January 1985), showing the extent of progradation since April 1939. The pecked lines indicate foredunes formed successively between 1939 and 1975, and the dotted area hummocks with *Cakile maritima* on sandy terrain added since 1975.

stage 2 was outflanked and extended as a recurved spit (stage 3). By stage 4, there had been progradation south of Somers (a in Fig. 8), forming a lobe which has since been cut away by erosion. Stage 5 was marked by further eastward growth, subsequently truncated by erosion of the eastern shore, where reeeding cliffs are undermining dune woodland. By stage 6 the coastline had become markedly sinuous, and included a lobe south of Western Park (b in Fig. 8), which has also since been removed. Stage 7 saw a further outgrowth, bringing the coastline to approximately the configuration found by European explorers.

The outline of Sandy Point was first shown on a sketch-map drawn by George Bass when he discovered Western Port in 1798. Slightly different versions appear on charts compiled subsequently by Flinders in 1799, Barrallier in 1801, Faure in 1802, D'Urville in 1826 and Weatherall in 1827, but it is doubtful if the discrepancies indicate actual changes of the coastline, for none of these charts was based on detailed surveys. The first map based on triangulation, by Smythe in 1842, showed an almost straight, slightly sinuous coastline like that of stage 7, and similar outlines appeared on charts produced by Stokes in 1843 and Cox in 1865.

Stage 8, attained early in the present century, included two small lobes (c and d in Fig. 8), which can

be seen on air photographs taken in 1939. These have since moved eastward (c to the grassy sector at Navy Beach, and d to Cormorant Point). By 1939 the coastline extending 1 km west from Sandy Point had been cut back to form a prominent dune cliff, which is still clearly traceable behind the more recent dunes east of Cormorant Point (Fig. 9).

Air photographs taken in 1939, 1956, 1968 and 1984 (Fig. 10) can be used to trace subsequent changes. At Cormorant Point (C) erosion of the southern flank has been accompanied by accretion and successive dune ridge formation on the eastern flank, and at Sandy Point (S) there has been rapid progradation (Fig. 11), especially since 1972, forming a broad cusped feature on the southern shore (Figures 12 and 13). The eastern shore has changed little, because of the strong ebb currents, which have inhibited eastward growth. Between 1956 and 1968 there was some progradation here, with the development of grassy dunes, but these have been cut away in the past few years, the sand having drifted both northwards (to widen and extend the spit that curves into the salt marsh basin behind Sandy Point) and southwards (to the bars and shoal that run south-west to Middle Bank).



Fig. 12—An oblique aerial view of Sandy Point (S) looking west to Cormorant Point (C), on 1 October 1972. Comparison with Fig. 13 will indicate that progradation has subsequently occurred on the southern shore of Sandy Point, and that the eastern shore has been cut back. Photo: Neville Rosengren.

Fig. 10—Changes in the coastline at Sandy Point (S) and Cormorant Point (C) shown on successive air photographs (Crown Copyright Reserved).



Fig. 13—An oblique aerial view of Sandy Point (S) looking west towards Cormorant Point (C), with Somers in the distance, 15 February 1984. Note the new foredunes on the recently-prograded area on the southern shore of Sandy Point. Photo: Neville Rosengren.

CHANGES SINCE 1975

Field observations of changes along the Somers-Sandy Point coastline were initiated by the author in 1966, with mapping of the extent of receding coastline (beach backed by cliffed dunes) and advancing coastline (beach backed by incipient foredunes). Erosion has been prevalent over the ensuing period, except on sectors at Navy Beach, Cormorant Point, and Sandy Point (Fig. 2) where accretion of sand has taken place.

In January 1975, a series of 24 transects was established between Somers and Sandy Point in order to measure rates of change (Fig. 14). Fixed datum posts were inserted a short distance inland, and repeated surveys from these were used to measure the advance or retreat of the coastline. On advancing sectors the coastline was taken as the seaward limit of dune vegetation, and on retreating sectors the base of the dune cliff was

used; both are roughly equivalent to the limit of the highest spring tides. The surveys, using level and staff, ran out to the low spring tide line.

The January 1985 surveys of these 24 transects were compared with profiles recorded a decade previously to show the extent of coastline advance or retreat. Cross-sectional areas measured on adjacent transects were averaged, and multiplied by the intervening distance to give an estimate of the volume of sand gained or lost over this period. The results are summarised in Table 1.

In 1976, the Division of Ports and Harbors (Public Works Department) inserted a series of poles along the shore at Somers (Fig. 6) to monitor beach changes there. With reference to these poles, it has been observed that Balnarring Beach has subsequently prograded, that the sector between the mouth of Merriicks Creek and Somers Point has been cut back, that the bay

TABLE 1
CHANGES ON THE SOMERS-SANDY POINT COASTLINE, 1975-1985.

Transect	Advance or Retreat (m)	Cross- Sectional Area (m ²)	Compartment	Mean Advance or Retreat (m)	Mean Cross- Sectional Area (m ²)	Width (m)	Area gain or loss (m ²)	Volume gain or loss (m ³)
A	-3.2	-1.8	AB	-8.4	-11.1	225	-1890	-2498
B	-13.6	-20.4	BC	-12.05	-24.45	225	-2711	-5501
C	-10.5	-28.5	CD	-15.3	-54.25	225	-3443	-12206
D	-20.1	-80.4	DE	-20.75	-102.2	225	-4669	-22995
E	-21.4	-124.0	EF	-16.3	-90.1	225	-3668	-20273
F	-11.2	-56.2	FG	-7.35	-30.9	225	-1654	-6953
G	-3.5	-5.6	GH	-3.25	-3.6	225	-731	-810
H	-3.0	-1.6	HI	-3.75	-5.0	225	-844	-1125
I	-4.5	-8.4	IJ	-6.0	-15.85	225	-1350	-3566
J	-7.5	-23.3	JK	-6.75	-22.7	225	-1519	-5198
K	-6.0	-22.2	KL	-4.0	-13.8	225	-900	-3105
L	-2.0	-5.4	LM	-3.55	-10.5	225	-799	-2363
M	-5.1	-15.6	MN	-4.3	-12.85	225	-968	-2891
N	-3.5	-10.1	NO	-2.3	-6.4	225	-518	-1440
O	-1.1	-2.7	OP	+2.6	+15.15	225	+585	+3409
P	+6.2	+33.0	PQ	+12.75	+49.75	225	+2869	+11194
Q	+19.3	+66.5	QR	+8.65	+31.15	225	+1946	+7009
R	-2.0	-4.2	RS	-2.9	-5.2	225	-653	-1170
S	-3.8	-6.2	ST	-3.5	-15.7	225	-788	-3533
T	-3.2	-25.2	TU	+7.15	+8.75	225	+1609	+1969
U	+17.5	+42.7	UV	+28.3	+39.65	225	+6368	+8921
V	+39.2	+36.6	VW	+40.9	+82.5	225	+9203	+18563
W	+42.6	+128.4	WX	+48.95	+135.2	120	+5874	+16224
X	+55.3	+142.0	XY*	—	—	—	+5461	+16385
*Addition to cover new area east of transect X						Balance	+6810	-11863

	AREA (m ²)		VOLUME (m ³)	
Total losses A-O	-25664		-90834	
Total losses R-T	-1441		-4703	
	<u>-27105</u>		<u>-95537</u>	
Total gains O-R	+5400		+21612	
Total gains T-X	+23054	+28515	+45677	+62062
Added for XY	+5461		+16385	
	<u>+33915</u>		<u>+83674</u>	
BALANCE	<u>+6810</u>		<u>-11863</u>	

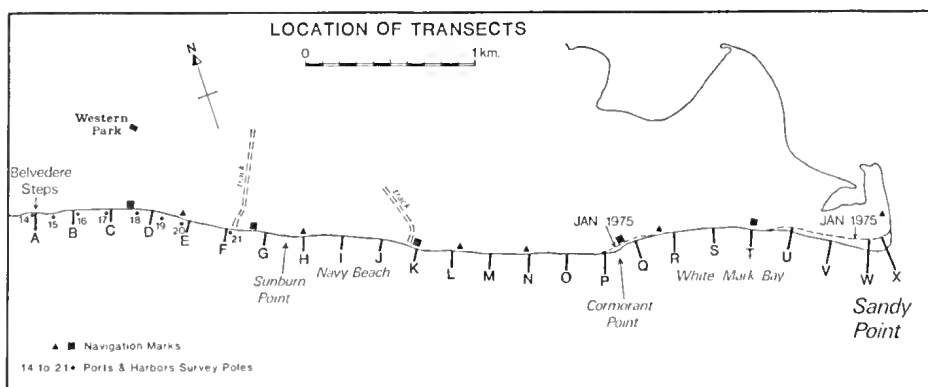


Fig. 14—Location of surveyed transects (A to X) on the Somers-Sandy Point beach, used in the preparation of Table 1. Positions of Ports & Harbors' poles (15 to 21) are also shown. The pecked line indicates the 1975 coastline at Cormorant Point and Sandy Point.

immediately east of Somers Point has shown minor backshore accretion, and that the dune cliff east of Belvedere Steps has retreated rapidly. In the latter sector, Ports and Harbors poles 15 to 21 cover almost the same stretch of beach as transects A to F in the author's survey, and measurements from these have shown similar rates of coastline recession.

Before analysing the results of the survey between Somers and Sandy Point (Table 1), some limitations are noted. The transects extended only to the low spring tide line, so that any gains or losses seaward of this line are not included. The input of eastward drifting sand to the surveyed area past transect A during the decade was not assessed, but was probably small because this was a period of accretion in the bay to the west. In places where the orientation of the coastline changed during the decade as the result of erosion or accretion, the transects did not remain orthogonal to the beach. On the foreland at Sandy Point the changes were so great that a supplementary survey was necessary to calculate the area and volume of accretion, in order to complete Table 1. In view of these limitations, the results obtained are considered to be only a general indication of the scale of changes that occurred here during the period 1975-1985.

The results show that the coastline retreated by up to 21.4 m on eroding sectors, and advanced by up to 55.3 m on accreting sectors, over this decade. On a beach 5.07 km long, an area of 2.7 ha of sandy terrain had been lost by erosion, and almost 3.4 ha gained by deposition. Erosion was most extensive on the 3.15 km sector east of Somers, and although there were limited sectors of temporary accretion (notably at Navy Beach) the only sustained accretion was at Cormorant Point and Sandy Point. The newly-deposited land is generally lower in elevation than the preceding land, removed by erosion.

In volumetric terms the sand removed from eroded sectors totalled about 95,500 m³, and the sand added to

prograded sectors about 83,700 m³. The balance of about 11,800 m³ lost from the Somers-Sandy Point beach system over this decade included sand blown from the beach to backshore dunes behind the 1975 coastline; sand carried round Sandy Point to be deposited on the small spit to the north; and sand swept offshore by wave scour, and especially by ebb currents at Sandy Point. It appears that much of the lost sand has been carried out on to the bars and shoals south-west of Sandy Point.

Progradation on Sandy Point between January 1975 and January 1985 resulted from deposition of about 62,000 m³ of sand, largely supplied by eastward longshore drifting, although a small amount was brought onshore from the adjacent shoals during brief periods of south-easterly wave action. The large volume of accretion here greatly exceeds the losses in the bay immediately to the west (compartments RS and ST), so that much of the sand has come alongshore from eroding sectors west of Cormorant Point. It is deduced that mean net longshore drifting of sand eastwards to Sandy Point has been at least 6,000 m³.y⁻¹.

In the course of these surveys, it was noted that erosion took place mainly during stormy periods, especially when strong wave action from the south-west accompanied a high spring tide. Under these conditions, waves attacked the base of the dune cliff, undermining grass tussocks, shrubs and trees. Erosion was particularly severe in the winter of 1981 (Power 1982). One storm, in June 1981, resulted in nearly 2 m of cliff recession on transect E in a single day. After such an event, the dune cliff is almost vertical and the beach profile smooth and evenly sloping down to the low spring tide line (Fig. 15, E), beyond which sand bars may be seen in the nearshore zone; but these are soon swept away to the east by longshore currents. It was observed that dune cliff recession was accompanied by lowering of the beach face, so that the profile as a whole moved landward, the retreat of the high spring tide line being matched by landward movement of the low spring

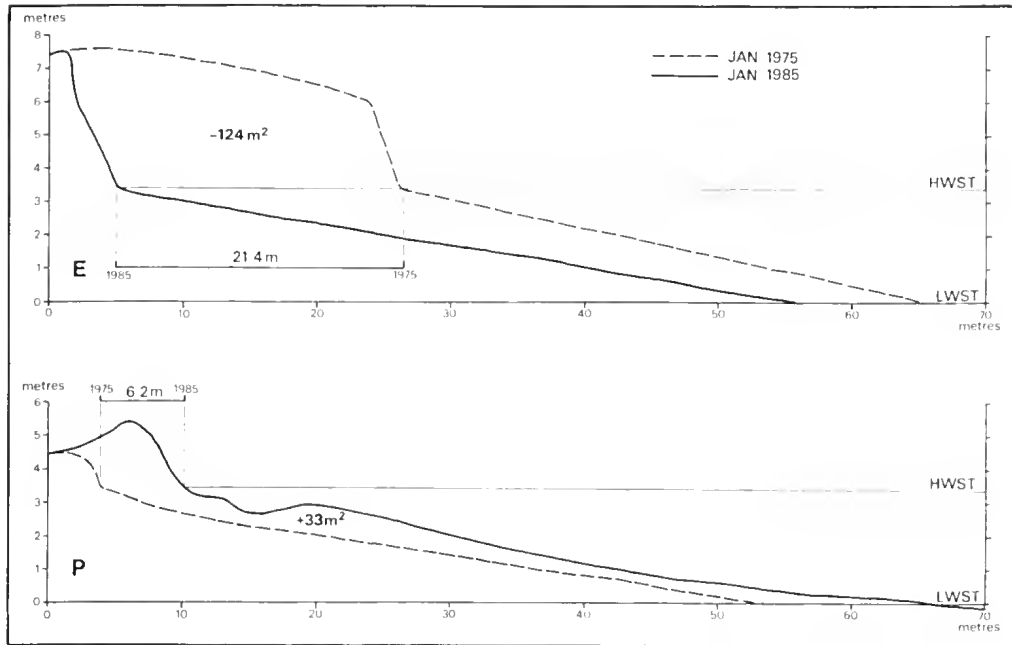


Fig. 15—Profiles on Transects E and P (for location see Fig. 14) in January 1975 and January 1985. Profiles at Transect E are typical of receding sectors, and those at Transect P of prograding sectors. The extent of advance or retreat is shown, together with cross-sectional areas between profiles, measured above low spring-tide level.

tide line. Off Navy Beach the presence of steep-sided, flat-topped residual sand banks bearing seagrass vegetation indicates that the nearshore sea floor may also have been dissected and lowered here.

Where progradation occurred, notably on the eastern flank of Cormorant Point and the southern shore of Sandy Point, the backshore showed incipient dune ridges and hummocks bearing *Cakile maritima*, *Spinifex hirsutus*, and marram grass (*Ammophila arenaria*): the latter became more extensive after it was planted on the dunes near Cormorant Point in the early nineteen-seventies, and in 1974 it colonised a beach ridge built by wave action east from Cormorant Point, thereafter trapping sand to build up a foredune which is now 2 to 3 m high (Bird 1985a: Fig. 2). On Sandy Point this prominent foredune marks the position of the backshore on the January 1975 coastline (Fig. 9).

On prograded sectors the upper beach, fronting foredunes, has an undulating topography, with layers of seagrass litter incorporated in the sand, which is loose and soft in texture, while the beach profile as a whole is gently-convex upward (Fig. 15, P). Beach accretion occurred mainly in the summer months, particularly when south-easterly winds were prevalent, generating waves which moved sand on to the shore, and winnowed dried beach sand to the backshore.

PREDICTIONS

On the basis of this ten-year survey, it is evident that losses from the Somers-Sandy Point beach system have exceeded gains. If this trend continues, a broad bay will be cut into the sandy foreland east of Somers, and sand eroded from this bay will drift eastwards, and be deposited on a growing foreland south from Sandy Point. It is possible that this evolution will be complicated by the development and eastward migration of further sand lobes: the backshore accretion in the bay east of Somers Point (South Beach Road) in the past decade may be a prelude to this.

Although it is possible that sand now in the bars and shoals extending from Sandy Point south-west to Middle Bank may eventually move back on to the shore, there has been no evidence of this in the past decade. The Somers-Sandy Point beach system has shown a prevalence of erosion during this period, consistent with the demonstrated modern trend on the world's sandy coastlines (Bird 1985b). In the next phase of research it is hoped that more detailed investigation of the nearshore and offshore morphodynamics in the south-west of Westernport Bay will elucidate the long-term future of the Somers-Sandy Point beach.

ACKNOWLEDGEMENTS

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NEREIS AND PLATYNEREIS (POLYCHAETA: NEREIDIDAE) FROM VICTORIA WITH DESCRIPTION OF A NEW SPECIES OF NEREIS

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ABSTRACT: *Nereis apalie* sp. nov. is described from Bass Strait. *Nereis parabifida* Hutchings & Turvey is synonymised with *Nereis bifida* Hutchings & Turvey. A systematic account of *Nereis* known from Victoria and a key to species recorded from southern Australia is provided.

During the years 1979-1983 the Museum of Victoria (previously National Museum of Victoria) made extensive collections of soft-bottom benthos as part of a survey of the marine fauna of Bass Strait. This paper reports on nereidid polychaetes of the genera *Nereis* and *Platynereis* collected during that survey and on additional material from the collections of the Museum of Victoria. Previous studies by Wilson (1984 — *Neanthes*) and Hartmann-Schröder (in prep. — *Ceratonereis*) complete the taxonomic description of the nereidid fauna of Bass Strait.

MATERIALS AND METHODS

Sources for the collections used in this study are as follows: BSS prefixes refer to stations occupied during the Bass Strait Survey (Wilson & Poore in press); PPBES prefixes refer to Port Phillip Bay Environmental Study (Poore *et al.* 1975, Poore & Kudenov 1978); CPBS and WBES prefixes refer to studies of Westernport Bay (Ministry for Conservation 1975, Coleman *et al.* 1978); and, SBS refers to the N.S.W. Shelf Benthic Survey (Jones 1977). Registration numbers of material in the Museum of Victoria are prefixed NMV. Paratypes have been deposited in the Australian Museum, Sydney (AM registration numbers). Codes in brackets accompanying AMW material from South Australia, e.g. (04B), refer to collection data from Table 1 of Hutchings and Turvey (1982).

The Australian distribution of each species is based on Hutchings and Turvey (1982) and new records presented here. Full Australian synonymies can be found in Day and Hutchings (1979). A key is provided to all species of *Nereis* known from south-eastern Australia, including four species (denoted in the key by an asterisk) which were recorded by Hutchings and Turvey (1982) from southern Australia but were not encountered in the collections reported on here.

SYSTEMATICS

Genus *Nereis* Linnaeus 1758

DIAGNOSIS: Eversible pharynx with conical paragnaths on both rings, may be few and sparse. Four pairs of tentacular cirri; parapodia biramous. Notosetae include

homogomph spinigers and falcigers, the latter in median and posterior setigers; neurosetae include homo- and heterogomph spinigers and heterogomph falcigers (after Fauchald 1977a).

TYPE SPECIES: *N. pelagica* Linnaeus 1758.

Nereis apalie sp. nov.

Fig. 1A-E

MATERIAL EXAMINED: Holotype NMV F50298 Bass Strait, 9 km N of Wynyard, Tasmania, 40°10.9'S, 145°44.3'E, 75 m, muddy carbonate sand, Smith-McIntyre Grab, G. Poore and others on RV Tangaroa, 13 Nov. 1981 (Stn BSS 157). Paratypes NMV F50299, AM W199449-199450, 3 specimens from type locality, epibenthic sled. One paratype NMV F50300, Bass Strait 150 km N of Devonport, 39°48.6'S 146°18.8'E, 82 m, muddy carbonate sand, epibenthic sled.

DESCRIPTION: Holotype an anterior fragment of 90 setigers, 35 mm length, 1 mm width (excluding parapodia) at setiger 10. Colour in alcohol pale yellow-brown with no obvious markings. Prostomial length equal to width. Eyes small (.05 mm diameter), dark red. One pair of palps with palpostyles and one pair of antennae. Four pairs of tentacular cirri, longest extending back to setiger 4. Jaws stout, translucent brown, with 6 teeth. Pharynx with small pale brown conical paragnaths arranged as follows: I, II & III = O; IV = 4, 2; V = O; VI = 1, 1; VII-VIII = O.

Notopodia with two elongate lobes and a dorsal cirrus, all of approximately equal length on anterior 40 setigers. Both notopodial lobes persist in similar proportions posteriorly but with dorsal cirrus becoming proportionally longer than each lobe from about setiger 40. Neuropodia with two lobes, acicular lobe triangular, about three quarters as long as notopodia, ventral lobe more slender and about 1.3 times as long as acicular lobe anteriorly, neuropodial lobes equal in size posterior to setiger 40. Ventral cirrus approximately three-quarters as long as ventral neuropodial lobe throughout (Fig. 1A, B).

Setigers 1 and 2 uniramous, setiger 3 with noto- and neuroacicula but without notosetae. Notopodial homogomph spinigers present from setiger 4, homogomph

KEY TO SPECIES OF *NEREIS* FROM SOUTHERN AUSTRALIA

1. Areas VII-VIII of pharynx with fewer than 30 paragnaths2
Areas VII-VIII with more than 40 paragnaths8
2. Blade of notopodial homogomph falcigers bifid (with a single large lateral tooth of similar size to terminal tooth)3
Blade of notopodial homogomph falcigers with 1-3 lateral teeth smaller than terminal tooth or with many fine lateral teeth5
3. Neuropodial heterogomph falcigers normally in both supra- and subacicular fascicles4
Neuropodial heterogomph falcigers replaced entirely by heterogomph spinigers in many anterior parapodia*Nereis spinigera**
4. Oral ring of pharynx bare*Nereis maxillodentata*
Oral ring of pharynx with paragnaths*Nereis bifida*
5. Area VI with 0-2 paragnaths, Area VII-VIII with 0-3 paragnaths, notopodial lobes of similar proportions throughout6
Area VI with 2-9 paragnaths, Areas VII-VIII with 4-22 paragnaths, dorsal notopodial lobe reduced on posterior setigers7
6. Area VI with 1-2 paragnaths, blade of notopodial falcigers with 3-6 small lateral teeth*Nereis apalie* sp. nov.
Area VI bare, blade of notopodial falcigers with 1-3 large teeth*Nereis heirissonensis**
7. Blade of notopodial falcigers with 2 or more large lateral teeth, dorsal notopodial lobe reduced on posterior setigers*Nereis denhamensis*
Blade of notopodial falcigers with very fine lateral teeth (may appear smooth on some specimens), notopodial lobes of similar proportions throughout*Nereis cirriseta**
8. Area III with 10 or more paragnaths, Area V bare*Nereis triangularis**
9. Notopodial falcigers not present before setiger 10, dorsal notopodial lobe reduced to a small digitiform process posteriorly*Nereis jacksoni*
Notopodial falcigers present from setiger 3, notopodial lobes of similar proportions throughout*Nereis cockburnensis*

*These species were not present in the material studied here and are not treated in the systematic text.

falcigers with long, finely-toothed appendage appear in notopodia from setiger 22 (Fig. 1D, E). Neurosetae of all setigers include homogomph spinigers dorsally and heterogomph spinigers ventrally, heterogomph falcigers also present in dorsal fascicle from setiger 4 (Fig. 1C).

VARIATION: Variations not described for the holotype based on four paratypes, anterior fragments size range 46 setigers, 6 mm long, 0.3 mm wide to 53 setigers, 12 mm length, 0.8 mm wide. Small pale conical paragnaths on both rings, arranged as follows: I, II & III = 0, IV = 3-5; V = 0; VI = 1-2; VII-VIII = 0. Homogomph falcigers appear in notopodia at setiger 13 in the smallest paratype, NMV F50299, otherwise at setigers 18 to 22. None of the specimens examined is complete posteriorly, and none has obvious coelomic gametes.

REMARKS: *Nereis apalie* sp. nov. is one of several species of *Nereis* which show a reduction in the number of oral ring paragnaths, and possess sparsely, coarsely-toothed notopodial falcigers. Tabulated descriptions of this group of species were provided by Hutchings and Turvey (1982). Two of these species, *N. falcaria* (Willey 1905) and *N. panamensis* Fauchald 1977b have anteriorly-indented prostomia which distinguishes them from *N. apalie* in which the anterior margin of the prostomium is entire. *Nereis ovarius* Read 1980 differs by having paragnaths on Areas III and VII-VIII whereas these are bare in *N. apalie*. *Nereis apalie* can be distinguished from all remaining similar species using the characteristics given in Table 1.

ETYMOLOGY: The specific name *apalie* is derived from an Australian aboriginal word meaning "of the sea".

DISTRIBUTION: Known only from two stations in central Bass Strait, southeastern Australia, 75-82 m depth.

HABITAT: Poorly-sorted, muddy-carbonate sediments incorporating much bryozoan skeletal remains.

Nereis bifida Hutchings & Turvey 1982

Fig. 2

1982 *Nereis bifida* Hutchings & Turvey pp. 116-119, fig. 9a-c.

1982 *Nereis parabifida* Hutchings & Turvey pp. 132-133, fig. 15a-c. New synonymy.

MATERIAL EXAMINED: W.A. — Aldritchs Cove, Nornalup, Dec. 1946, 72 specimens, AM W6174.

S.A. — Speeds Pt, Streaky Bay (04B), 14 Mar. 1979, 5 paratypes, AM W18359; Stokes Bay, Kangaroo Is. (20A), 5 Mar. 1979, 10 specimens, AM W18369; American River, Kangaroo Is. (27B), 2 Mar. 1979, 72 paratypes, AM W18365.

Tas. — 42°37'S, 148°20'E, 102 m, 9 Oct. 1983, 10 specimens, NMV F50275; 38°6.2'S, 149°45.5'E, 188 m 14 Oct. 1983, 2 specimens, NMV F50276, 43°25.3'S, 145°39.8'E, 160 m, 3 specimens, NMV F50277.

Bass Strait — Big Green Is, 12 Apr. 1983, 9 specimens, NMV F50253; Pegleg Cove, Deal Is, Apr. 1983, 5 specimens, NMV F50259-F50260. Stn BSS 107 SEB, 1 specimen, NMV F50263; Stn BSS 139 trawl, 2 specimens, NMV F50264; Stn BSS 163 SEB, 1 specimen, NMV F50265; Stn BSS 169 GSM, 1 male capitoc, NMV F50266; Stn BSS 170 GSM, 1 gravid female, NMV F50268; Stn BSS 170 SEB, 75 specimens, NMV F50269; Stn BSS 174 SEB, 7 specimens, NMV F50270; Stn BSS

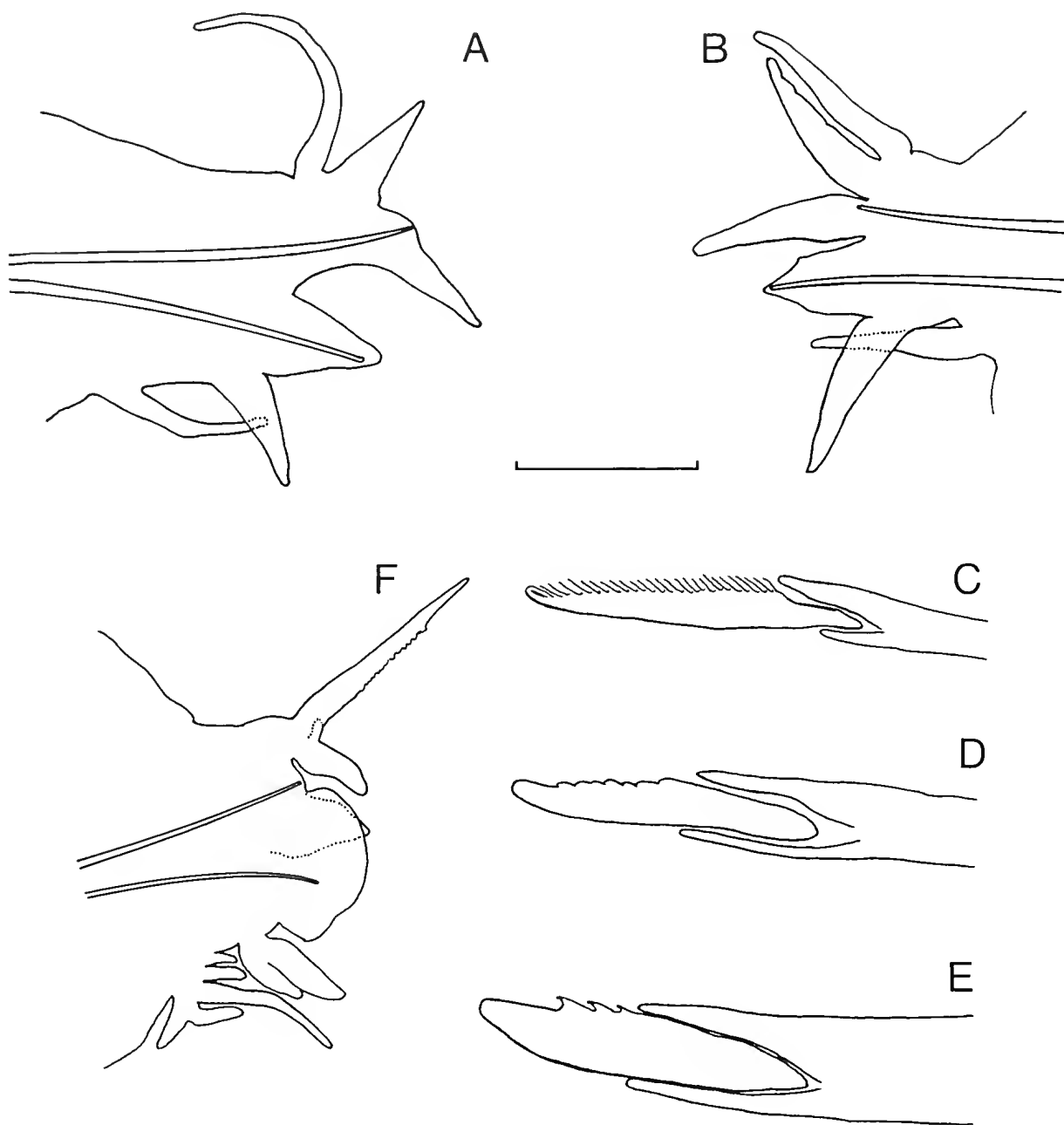


Fig. 1—A-E, *Nereis apalie* sp. nov., holotype NMV F50298. A, anterior view of 5th parapodium. B, posterior view of 74th parapodium. C, heterogomph falciger from dorsal neuropodial fascicle, setiger 5. D, notopodial homogomph falciger, setiger 26. E, notopodial homogomph falciger, setiger 74. F, *Nereis maxillodentata* Hutchings & Turvey 1982 NMV F50281. F, posterior view of 36th parapodium from immature male epitoke. Scale bar = 0.2 mm figs A, B, F; 0.02 mm figs C, D, E.

179 SEB, 1 specimen, NMV F50271; Stn BSS 207 SEB, 4 specimens, NMV F50272; Stn BSS 213 trawl, 10 specimens, NMV F50273; Stn BSS 217 trawl, 1 specimen, NMV F50274.

Vic. — Black Rock, Connewarre, 7 Nov. 1978, 2 specimens, NMV F50261 (Stn 1 of Dorsey & Synnot 1980); Portsea Pier, Port Phillip Bay, June 1977, 4 specimens, NMV F50257; Westernport Bay CPBS Stn 03S, 7 specimens, NMV F50246-50247; Sunderland Bay, Phillip Is, 3 Feb. 1979, 1 specimen, NMV F50256; Manns Beach, Corner Inlet, 19 Nov. 1983, 1 specimen, NMV F50262.

Nereis parabifida S.A. — Cape du Coudic, Kangaroo Is. (30B), 4 Mar. 1979, 1 paratype, AM W18512.

NSW — Sydney, Shelf Benthic Survey, 26 Nov. 1973, holotype, AM W18511; Middleton Reef, 55-73 m, 26 Nov. 1960, 1 paratype, AM W4804.

REDESCRIPTION: Size range of material examined: 39 setigers, 11 mm long, 0.5 mm wide (anterior fragment) to 74 setigers, 24 mm long, 0.7 mm wide (entire specimen). Prostomial length 1.25 times width. Two pairs of eyes dark red to black. One pair of palps with palpostyles, 1 pair of antennae; palps and antennae approximately equal in length to prostomium. Four pairs of tentacular cirri, longest extending to setiger 2-7. Pharynx with brown jaws with 6-8 teeth. Pale brown conical paragnaths arranged as follows: I = 0; II = 3-9; III = 0-3 in a single transverse row; IV = 5-10; V = 0; VI = 1-3; VII-VIII = 2-8 in a single transverse row. Anterior dorsum of many specimens often with a characteristic pattern of orange to brown bars (Fig. 2). Many specimens with faint pattern or unpigmented.

Notopodium with two lobes anteriorly, ventral lobe larger, dorsal lobe reduced to small tubercle or lost posteriorly, from about setigers 15-25. Dorsal cirrus approximately equal in length to larger notopodial lobe. Neuropodium with two approximately equal lobes throughout and ventral cirrus about three quarters length of neuropodium. Notosetae homogomph spinigers anteriorly, bifid homogomph falcigers appearing in notopodia from setigers 13-17. Neurosetae homogomph spinigers and heterogomph falcigers in the dorsal fascicle, heterogomph spinigers and falcigers in the ventral fascicle. Anal cirri extend over last 5-8 setigers.

REMARKS: *Nereis bifida* and *N. parabifida* were described by Hutchings and Turvey (1982) who separated the two species on the basis of differing arrangements of paragnaths primarily on Area III (0, occasionally 1 for *N. bifida*; 3-5 for *N. parabifida*) and Area VI (1, rarely 0 or 2-3 for *N. bifida*; 2-4 rarely 1 for *N. parabifida*). In respect of parapodia and the bifid homogomph falcigers the two species could not be separated.

The material examined in this study contains many specimens intermediate between the above two species. In addition, many specimens share a distinctive pigmented pattern on the anterior dorsum (Fig. 2). Examples of specimens with this pattern include typical *N. bifida* (*sensu* Hutchings & Turvey 1982): NMV

F50258-F50260, F50272; typical *N. parabifida*: NMV F50265, F50271; and intermediate forms NMV F50275, F50276. For these reasons I consider that the forms constitute a single species and *Nereis parabifida* is here synonymised with *N. bifida* and the description of *N. bifida* is expanded.

DISTRIBUTION: Western Australia, South Australia, Tasmania, Victoria, New South Wales. Known only from southern Australia.

HABITAT: Mostly subtidal from sediment, algae and seagrass. Occasionally intertidal.

Nereis cockburnensis Augener 1913

1913 *Nereis cockburnensis* Augener pp. 153-156, pl. 3 fig. 47, text figs 15a-c.

1971 *Nereis cockburnensis* Augener; Knox & Cameron p. 28.

1982 *Nereis cockburnensis* Augener; Hutchings & Turvey pp. 121-124, fig 4b.

MATERIAL EXAMINED: S.A. — Hanson Bay, Kangaroo Island, 4 Mar. 1979, 18 specimens, AM W18351; Sellicks Beach, 16 Mar. 1979, 9 specimens, AM W18355 (material of Hutchings & Turvey 1982). N side of West Island, 21 Mar. 1985, NMV F50313.

Bass Strait — Stn BSS 50 GSM, NMV F50307; Stn BSS 154 GSM & SEB, 2 specimens, NMV F50308; Stn BSS 187 DR, NMV F50309; Stn BSS 196 DP, NMV F50310; Stn BSS 199 GSM, NMV F50311; Stn BSS 201 GSM, NMV F50312.

Vic. — Port Phillip Bay Area 57 Stn 294, 1 specimen, NMV G1786 (material of Knox & Cameron 1971). Cape Wellington, Wilsons Promontory, 9 Feb. 1982, 1 specimen, NMV F50252; Hobbs Head, Wilsons Promontory, 9 Feb. 1982, 1 specimen, NMV F50255.

DESCRIPTION: Size range of material examined: 41 setigers, 5 mm length, 0.3 mm width to 37 setigers, 14 mm length, 1.0 mm width (anterior fragments). Tentacular cirri extend back 4-6 setigers. Paragnaths pale domes, arranged as follows: I = 0-1; II = 6-9; III = 1-4; IV = 12-16; V = 1-3; VI = 4-7; VII-VIII = 40-80 large and small cones in 2-4 rows. Paragnaths indistinct on small specimens (0.3 mm width).

Notopodia and neuropodia each with two approximately equal lobes throughout, ventral cirrus about equal to parapodia in length, dorsal cirrus 1.5-2 times parapodial length. Notopodial homogomph falcigers with long blades and many fine lateral teeth appearing from setiger 3 in most specimens, some material (NMV F50252, F50255) with notopodial falcigers present from setigers 6-9 but with many anterior notosetae broken. REMARKS: Six specimens from Bass Strait referred here to *Nereis cockburnensis* are too small to determine paragnath counts — identifications of these specimens are based on the presence of typical long-bladed homogomph falcigers in all notopodia commencing at setiger 3 (juveniles of other species of *Nereis* which lack characteristic setae are often indeterminable). No other known species of Australian *Nereis* has this character. All other material (including NMV F50309 from Bass Strait) agrees with the previous published descriptions

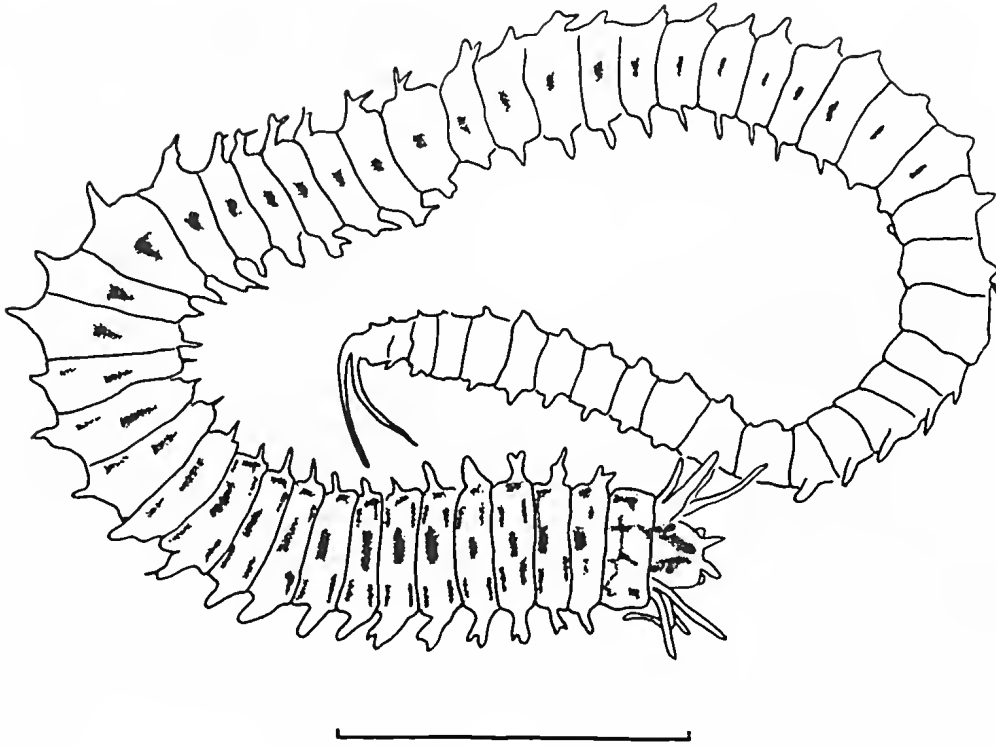


Fig. 2—*Nereis bifida* Hutchings & Turvey 1982. Dorsal view of whole worm, NMV F50258.

with the qualified exception of two specimens noted above where homogomph falcigers were not noted before setiger 6-9. This character is discussed further in the remarks section of *Nereis jacksoni* (below).

DISTRIBUTION: Western Australia, South Australia, Bass Strait, Victoria, New South Wales.

HABITAT: Associated with algae, encrusting fauna and subtidal soft sediments to 79 m.

Nereis denhamensis Augener 1913

1913 *Nereis denhamensis* Augener pp. 156-159, pl. 3 fig. 51, text fig. 16a-b.

1982 *Nereis denhamensis* Augener; Hutchings & Turvey pp. 124-5, fig. 11a-k.

MATERIAL EXAMINED: S.A. — Speeds Point, Streaky Bay, 14 Mar. 1979, AM W18546; Maston Point, Kangaroo Is. 2 Mar. 1979, AM W18548 (Material of Hutchings & Turvey 1982).

Bass Strait — Stn BSS 154 GSM & SEB, 1 specimen, NMV F50301; Stn BSS 159 GSM, 1 specimen, NMV F50302; Stn BSS 185 DR, 2 specimens, NMV F50304; Stn BSS 203 DR, 1 specimen, NMV F50306; Stn BSS 206, 4 specimens, NMV F50303.

Vic. — Wilsons Promontory S of Waterloo Point, 19 m, epibenthic sled, 8 Feb. 1982, 1 specimen, NMV F50305.

DESCRIPTION: Size range of specimens: 24 setigers, 3 mm length, 0.3 mm width (anterior fragment) to 56 setigers, 12 mm length, 0.7 mm width (entire specimen).

Tentacular cirri distinctly annulated, extend back to setigers 3-4. Pharynx with small dark brown domed paragnaths arranged as follows: I = 0-5; II = 4-13; III = 0-15; IV = 4-17; V = 0; VI = 2-9; each group generally in 2 rows; VII-VIII = 7-22 in 1 to 2 rows.

Notopodia with two approximately equal lobes anteriorly, dorsal lobe reduced to a small digitiform process posteriorly, from about setigers 10-16. Dorsal cirrus approximately 1-1.5 times notopodial length anteriorly, becoming 2-2.5 times notopodial length posteriorly, from about setigers 30-40. Neuropodia about equal in length to notopodia, with two lobes throughout, ventral lobe smaller and reducing posteriorly, from about setiger 30. Ventral cirrus about three quarters neuropodial length. Anal cirri extend back 4-5 setigers.

Notosctac homogomph spinigers anteriorly, homogomph falcigers appearing at setigers 11-18. Dentition of blade of homogomph falcigers variable, small specimens with 3-5 lateral teeth smaller than distal tooth, larger specimens with fewer larger lateral teeth often reducing to a single large lateral tooth on posterior setigers.

REMARKS: The material examined in this study extends the range of variability of *Nereis denhamensis* noted by Hutchings and Turvey (1982). Many specimens are small (less than 0.5 mm wide excluding parapodia) and these specimens account for the low paragraph counts recorded (I = 0-1, III = 0-1). This is the first record of *N. denhamensis* from Victoria.

DISTRIBUTION: Western Australia, South Australia, Bass Strait, Victoria.

HABITAT: Intertidally among algae, seagrasses, sponges and rocks (Hutchings & Turvey material); soft bottom benthos of Bass Strait to 80 m depth.

Nereis jacksoni Kinberg 1866

Fig. 3A-C

1866 *Nereis jacksoni* Kinberg p. 169.

1922 *Nereis jacksoni* Kinberg; Augener pp. 18-19 (re-examination of type material).

1982 *Nereis jacksoni* Kinberg; Hutchings & Turvey pp. 129-130, fig. 13 (re-examination of type material).

MATERIAL EXAMINED: Vic. — Black Rock Connemara (Stn 3 of Dorsey & Synnot 1980), 11 Jan. 1977, 1 specimen, NMV F50314.

Bass Strait — Stn BSS 166 SEB, 1 specimen, NMV F50315; Stn BSS 178 SEB, 1 specimen, NMV F50316.

DESCRIPTION: Size range: 56 setigers, 12.5 mm length, 0.8 mm width (entire specimen) to 26 setigers, 13 mm length, 1.5 mm width (anterior fragment). Colour in alcohol pale brown with no obvious markings. Prostomial length about equal to width. Two pairs of red to black eyes, one pair of antennae, one pair of palps with large palpostyles. Four pairs of tentacular cirri distinctly annulated, longest extending to setiger 3. Jaws pale brown with 6-7 teeth. Pharynx with pale brown conical paragnaths on both rings, arranged as follows: I = 0-1; II = 8-10; III = 1-3; IV = 12-18; V = 2-7; VI = 4-5; VII-VIII = 43-100 in 2-4 rows, narrowing to 1-2 rows laterally.

Notopodia with two lobes, dorsal lobe smaller and gradually reducing posteriorly from about setigers 15-25 but persisting as a small digitiform process on posterior-most setigers. Dorsal cirrus about 1.5 times notopodial length anteriorly, about 2 times notopodial length posteriorly, from about setiger 20. Neuropodia equal in length to notopodia, consisting of two equal lobes and a ventral cirrus of about equal length, proportions remaining constant on all setigers. Notosetae homogomph spinigers anteriorly, homogomph falcigers appearing at setigers 10-16 and replacing spinigers posteriorly. Neurosetae heterogomph spinigers and falcigers in ventral fascicle, homogomph spinigers and heterogomph falcigers in dorsal fascicle. Homogomph falcigers with long blades and many fine lateral teeth when they first appear, blades becoming shorter and with fewer larger lateral teeth posteriorly (Fig. 3A-C). One pair of anal cirri extending back 5-6 setigers.

REMARKS: Hutchings and Turvey (1982) redescribed *Nereis jacksoni* based on Kinberg's type material (a single specimen to two fragments). They were unable to identify any subsequent records as *N. jacksoni* and referred many subsequent records to a variety of different species. Of the records of *N. jacksoni* cited in Day and Hutchings (1979), four Australian records remain and require verification: Augener (1927), Monro (1936), Monro (1939) and Rullier (1965) [Day & Hutchings give Knox & Cameron (1971) as an additional record of *N. jacksoni*; this is an error as Knox &

Cameron's paper makes no mention of *N. jacksoni*]. *Nereis jacksoni* is known in Australia only from the holotype and the three specimens from Bass Strait reported in this paper.

The new Bass Strait material examined here is referred to *Nereis jacksoni* on the basis of paragnath counts, shape of parapodia and shape of notopodial falcigers, all of which agree with the redescription given by Hutchings and Turvey (1982). This species also appears to be close to *Nereis cockburnensis* Augener 1913, particularly in paragnath counts and in the form of the homogomph falcigers which have long fine-toothed blades when they first occur in anterior notopodia. The two species differ in the development of the dorsal notopodial lobe which is reduced posteriorly in *N. jacksoni* but is fully developed throughout in *N. cockburnensis*. The presence of notopodial homogomph falcigers from setiger 3 in *N. cockburnensis* also distinguishes that species from *N. jacksoni* (and all other Australian species of *Nereis*) in which notopodial homogomph falcigers do not appear before setiger 10. This character must be assessed cautiously in specimens with broken setae, however the three specimens here referred to *N. jacksoni* have intact anterior notosetae which consist of homogomph spinigers only before setigers 13-16 (one specimen has a single homogomph falciger at setiger 10 but no further notopodial falcigers until setiger 13). These specimens thus cannot be *N.*

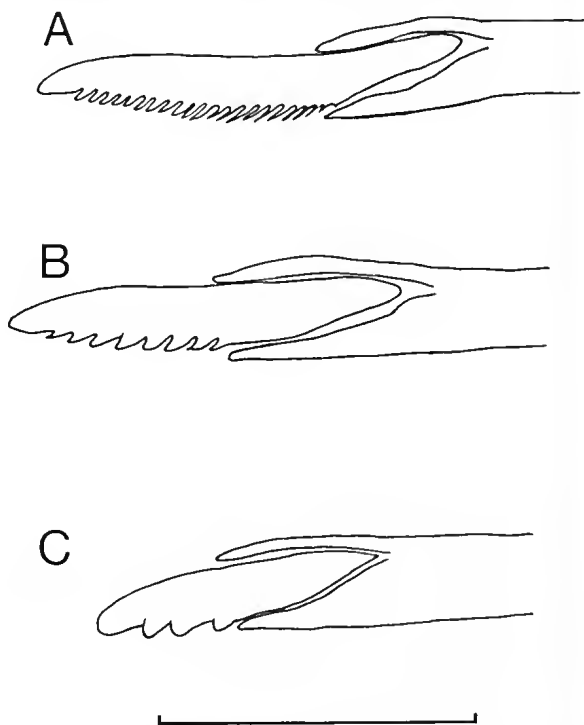


Fig. 3—*Nereis jacksoni* Kinberg 1866 NMV F50315. A, notopodial homogomph falciger, setiger 15. B, notopodial homogomph falciger, setiger 23. C, notopodial homogomph falciger, setiger 52. Scale bar = 0.04 mm.

cockburnensis as presently defined. This character may be variable however, and several specimens of *N. cockburnensis* examined in this study may not possess notopodial faleigers before setigers 6-9 although the determination is equivocal as some anterior notosetae were broken (see remarks section on *Nereis cockburnensis*).

Nereis jacksoni is known only from four records in eastern Australia while *N. cockburnensis* is widespread in South Australia and Western Australia with a few records in eastern Australia. More material is required from south-eastern Australia to clarify the differences between these two species and to determine the exact range of both species.

DISTRIBUTION: Port Jackson, New South Wales (type locality), Bass Strait, Victoria.

HABITAT: Rocky intertidal shores (Port Jackson), rock and soft sediments to 26 m (Bass Strait).

Nereis maxillodentata Hutchings & Turvey 1982

Fig. 1F

1971 *Ceratonereis costae* (Grube 1840); Knox & Cameron p. 27. (misidentification).

1971 *Platynereis australis* (Schmarda 1861); Knox & Cameron, p. 28 (misidentification, in part)

1982 *Nereis maxillodentata* Hutchings & Turvey pp. 130-2, fig. 14a-c.

MATERIAL EXAMINED: Bass Strait — Stn BSS 51 GSM, gravid female NMV F50290; Stn BSS 113 SEB, 2 specimens, NMV F50291; Stn BSS 160 SEB, 1 specimen, NMV F50292; Stn BSS 173 SEB, 2 specimens, NMV F50293; Stn BSS 188 GSM, 1 specimen, NMV F50294; Stn BSS 199 DR, 2 specimens, NMV F50295; Stn BSS 203 GSM, 1 specimen, NMV F50296; Stn BSS 204 DR, 1 specimen, NMV F50297. Additional material, NMV unregistered: Stns BSS 64, 139, 161, 166, 170, 176, 177, 178, 185, 190, 191, 194, 198, 199, 212 (total of about 50 specimens).

Vic. — Black Rock, Connewarre, Stn 3 of Dorsey and Synnot (1980), 1 specimen, NMV F50284. Port Phillip Bay: Portsea Pier, June 1977, 4 specimens, NMV F50257. Port Phillip Survey Area 7 Stn 207 NMV G1903, Area 11 Stn 212 NMV G1763, Area 29 Stn 107 NMV G1760, Area 69 Stn 97 NMV G1898, 5 specimens identified as *Ceratonereis costae* by Knox and Cameron

TABLE 1

COMPARISON OF AUSTRALIAN SPECIES OF *NEREIS* WITH REDUCED ORAL RING PARAGNATHS

	Area II	Area III	Area VI	Area VII-VIII	Condition of notopodial faleigers	Condition of dorsal notopodial lobe	Source of data
<i>N. apalie</i> sp. nov.	0	0	1-2	0	blade with 3-6 small lateral teeth	present all setigers	this study
<i>N. bifida</i> Hutchings & Turvey 1982	0	0-3	1-3	2-8	bifid, blade with a single large lateral tooth	reduced or absent posteriorly	this study, Hutchings & Turvey 1982
<i>N. cirriseta</i> Hutchings & Turvey 1982	2-5	0-1	1-6	4-7	blade with many small lateral teeth	present all setigers	Hutchings & Turvey 1982
<i>N. denhamensis</i> Augener 1913	4-13	0-15	2-9	7-22	blade with 1-5 large lateral teeth	reduced or absent posteriorly	this study, Hutchings & Turvey 1982
<i>N. heirissonensis</i> Augener 1913	0-1	0	0	0-3	blade with 1-3 large lateral teeth	reduced or absent posteriorly	Hutchings & Turvey 1982
<i>N. maxillodentata</i> Hutchings & Turvey 1982	2-7	0-4	0	0	bifid, blade with a single large lateral tooth	reduced or absent posteriorly	this study, Hutchings & Turvey 1982
<i>N. spinigera</i> Hutchings & Turvey 1982	0-3	0	0-1	2-7	bifid, blade with a single large lateral tooth	absent all setigers	Hutchings & Turvey 1982

(1971). Port Phillip Survey Area 5 Stn 53, NMV G1899, Area 14 Stn 175 NMV G1907, Area 31 Stn 10 NMV G1775, Area 40 Stn 101; 6 specimens, part of material identified as *Platynereis australis* by Knox and Cameron (1971). Westernport: Flinders pier, 26 May 1970, 9 specimens, NMV F50249; Crawfish Rock, 13 Oct. 1968, 4 specimens, NMV F50251; CPBS Stn 22N, 1 specimen, NMV F50287; CPBS Stn 32N, 1 specimen, NMV F50288; CPBS Stn 33S, 27 specimens NMV F50289. Corner Inlet: 9.5 km SW Port Albert, 23 Nov. 1983, 9 specimens, NMV F50281; 4 km SW Barry Beach, 24 Nov. 1983, 1 specimen, NMV F50282.

NSW — Burrewarra Point, Apr. 1984, NMV F50280.

DESCRIPTION: Size range of material examined: 41 setigers, 8 mm length, 0.4 mm width to 104 setigers, 23 mm length, 1.2 mm width. Paragnaths brown cones, restricted to maxillary ring, arranged as follows: I = O; II = 1-5; III = 0-2; IV = 2-9. Bifid homogomph falcigers appear in notopodia at setigers 15-19. Several specimens with orange-pigmented bands dorsally on apodous segment and prostomium.

Male epitoke (NMV F50281) with enlarged eyes, dorsal cirri inflated basally over setigers 1-7; ventral cirri inflated over setigers 1-5. Epitokous modifications of parapodia commencing setiger 16. Ventral surface of dorsal cirri crenulate over middle setigers. One large lobe and one small digitiform lobe located ventrally at base of dorsal cirrus. Dorsal notopodial lobe lost, ventral notopodial lobe produced into a roughly triangular lappet. Neuropodium consists of a large lamellar lobe containing the aciculum, and a pair of digitiform lobes ventrally. Ventral cirrus smooth. Two pairs of digitiform lobes located dorsally and ventrally at the base of the ventral cirrus (Fig. 1F). No natatory setae present. One gravid female (NMV F50290) with large eggs (350-400 μ m) in coelom. Eyes enlarged, almost touching but no other epitokal modifications.

REMARKS: The material examined in this study agrees with the original description of Hutchings and Turvey (1982) although many specimens, particularly those from Bass Strait, have paragnath counts at the lower limit of the range given above. This species appears to be closely related to *N. bifida* Hutchings & Turvey and several specimens are pigmented on the anterior dorsum in a similar manner to that species (e.g. NMV F50296) however the presence of oral ring paragnaths clearly distinguishes *N. bifida* from *N. maxillidentata*. *Nereis maxillidentata* is the most abundant species of *Nereis* in subtidal to continental shelf soft sediments in south-eastern Australia.

DISTRIBUTION Victoria, New South Wales, Queensland.

HABITAT: Subtidally in algae and encrusting invertebrates, soft bottoms to 115 m.

Genus *Platynereis* Kingberg 1866

DIAGNOSIS: Eversible pharynx with paragnaths on both rings, including cones and pectinate bars. Four pairs of tentacular cirri; parapodia biramous. Notosetae include homogomph spinigers and falcigers, the latter some-

times fused to form simple falcigers; neurosetae include homo- and heterogomph spinigers and heterogomph falcigers (after Fauchald 1977a).

TYPE SPECIES: *P. magalhaensis* Kinberg 1866.

Platynereis dumerilii antipoda Hartman 1954

1954 *Platynereis dumerilii antipoda* Hartman pp. 35-36, fig. 33-37.

1971 *Platynereis australis* (Schmarda 1861); Knox & Cameron, p. 28 (in part, see below).

1982 *Platynereis dumerilii antipoda* Hartman; Hutchings & Turvey p. 141.

MATERIAL EXAMINED: W.A. — King George Sound, 4 Apr. 1984, 4 m, red algae, 1 specimen, NMV F50220; Vancouver Peninsula, 8 Apr. 1984, 7 m, *Halophila*, 1 specimen, NMV F50221; Thistle Cove, 11 Apr. 1984, 8 m, brown and coralline algae, 2 specimens, NMV F50222; Lucky Bay, 12 Apr. 1984, 5 m, red algae, 5 specimens, NMV F50223.

Bass Strait — Stn BSS 110 SEB, 4 specimens, NMV F50206; Stn BSS 166 SEB, 1 specimen, NMV F50207; Stn BSS 193 DR, 1 specimen, NMV F50208; Stn BSS 207 SEB, 4 specimens, NMV F50209; Stn BSS 208 SEB, 1 specimen, NMV F50210; Stn BSS 212 SEB, 5 specimens, NMV F50211; Ransonnnet Bay, 40°40'S, 145°00'E, 3 Nov. 1980, 1 male epitoke, NMV F50159.

Vic. — Port Phillip Bay: Area 5 Stn 169, 1 specimen, NMV G1902; Area 9 Stn 178, 1 specimen, NMV G1688; Area 42 Stn 38, 4 specimens, NMV G1776; Area 59 Stn 36, 1 specimen NMV G1779; Area 63 Stn 20, 1 specimen, NMV G1906 [material identified as *P. australis* (Schmarda, 1861) by Knox & Cameron, 1971]. Altona, Port Phillip Bay, coll. Sept. 1964, 1 specimen, NMV F50117. Westernport Bay, WPBES: Stn 1704, 3 specimens, NMV F50127; Stn 1709, 3 specimens, NMV F50125; Stn 1723, 1 specimen, NMV F50124; Stn 1735, 3 specimens, NMV F50126. Westernport Bay, Crib Point, CPBS: Stn 03N, 7 specimens, NMV F50212; Stn 11S, 3 specimens, NMV F50213; Stn 31N, 2 specimens, NMV F50214; Stn 100, 2 specimens, NMV F50215. Wilsons Promontory: Hobbs Head, 9 Feb. 1982, 13 m, 1 specimen, NMV F50121; 2 km W of Growlers Ck., 5 Feb. 1982, 21 m, 1 specimen, *Zostera*, epibenthic sled, NMV F50122; bay S of Waterloo Point, 18 Feb. 1982, 19 m, 3 specimens, brown algae, epibenthic sled, NMV F50116. Corner Inlet: 3.5 km SE Port Albert, 22 Nov. 1983, 11 specimens, NMV F50216; Shelter Cove, 23 Nov. 1983, 2 specimens, NMV F50217; 38°43'S, 146°20'E, 24 Nov. 1983, 4 specimens including 1 male epitoke NMV F50218.

N.S.W. — Burrewarra Point, Apr. 1984, 14-17 m, 5 specimens, NMV F50224-5. Woolgoolga, July 1973, kelp holdfasts, 1 specimen, NMV F50226.

DESCRIPTION: Size range: 25 setigers, 4 mm length, less than 1 mm width (entire specimen) to 53 setigers, 31 mm length, 3 mm width (anterior fragment). Pharynx with paragnaths as pectinate bars on both rings, arranged as follows: Area I = O, II = O, III-up to 3 groups of short transverse bars; IV = 3-5 bars, several incomplete, forming a triangular or crescentic patch, V = O, VI-up

to 2 short transverse bars, VII-VIII = 3-5 short transverse bars.

Parapodial lobes globose over setigers 4-10, becoming elongate cones posteriorly. Notopodia from setiger 3 with two approximately equal lobes and basally attached dorsal cirrus about 1.5 times length of notopodia. Neuropodia with two lobes, ventral lobe longer than acicular lobe. Digitiform neuropodial postsetal process present except over setigers 4-10. Ventral cirrus basally attached, about three quarters length of neuropodia. Notosetae homogomph spinigers, homogomph falcigers present also over a variable number of posterior segments. Neurosetae homogomph spinigers and heterogomph falcigers in the dorsal fascicle and heterogomph spinigers and falcigers in the ventral fascicle.

Immature male epitoke (NMV F50218) with epitokal modifications appearing gradually at about setiger 20 but with crenulate dorsal cirri from setiger 15. Bases of dorsal cirri inflated over setigers 1-7 and of ventral cirri over 1-4. Lamellar lobes present dorsally to dorsal cirrus, dorsally and ventrally to ventral cirrus and postsetally in the neuropodium from about setiger 22. Tentacular and anal cirri extend over 16 and 18 setigers respectively. Natatory setae absent.

REMARKS: The material examined in this study agrees with the description of South Australian material by Hutchings and Turvey (1982), notably in the variability of the paragnaths on III which may be reduced or absent (especially on smaller specimens) and in the degree to which the blades of the notopodial falcigers are notched distally. The position at which notopodial falcigers are first present was also found to vary considerably and appears to be independent of size: homogomph falcigers may be present from setiger 25 (in an entire specimen of 49 setigers) or may be present only in the last 6-8 setigers. This is in contrast to the observations of Day (1967, 1975) and Imaijima (1972) on a closely-related species, *Platynereis australis* (Schmarda 1861), in which notopodial falcigers are reported to be present in juveniles but are lost in adults. Both Day and Imaijima accept that the absence of notopodial falcigers is the major character which distinguishes *P. australis* and *P. dumerilii*, although Hartman (1954) states that these two species also differ in the position at which modified parapodia appear in female epitokes.

All complete specimens examined in this study, including the material from Port Phillip Bay identified as *P. australis* by Knox and Cameron (1971), carried homogomph falcigers on a variable number of posterior notopodia and all are thus referred to *Platynereis dumerilii antipoda* Hartman 1954, following Hutchings and Turvey (1982). Both *Platynereis dumerilii antipoda* and *Platynereis australis* are duly reported from Australia (Day & Hutchings 1979).

DISTRIBUTION: Western Australia, South Australia, Tasmania, Victoria, New South Wales, Queensland. Also known from New Zealand.

HABITAT: Associated with algae and seagrass, usually on sheltered coasts, intertidal to 20 m. Also subtidally

(below wave action) on exposed coasts and infrequently from rocky substrates in Bass Strait to 95 m.

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FOSSIL BARNACLES (CIRRIPEDIA: THORACICA) FROM THE LOWER MIOCENE BATESFORD LIMESTONE, VICTORIA

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ABSTRACT: A cirriped fauna of 11 species (2 new), from the lower Miocene (Batesfordian) Batesford Limestone at Dog Rocks, Victoria, is described; it is the first record of these species from shallow water calcarenites.

Stratigraphic distribution of the cirripeds is analysed and is shown to be consistent with a gradual and apparently continuous marine transgression in the region. The absence of both the Chthamaloidea and the Balaninae is appraised, and reasons for this are proposed, with consideration given to the knowledge that both taxa were extant in the Miocene.

During the early Miocene, sediments of the Batesford Limestone were deposited on the flanks of Dog Rocks, a granitic pluton about 8 km northwest of Geelong, Victoria. The material discussed in this paper comes from a vertical sequence through the type locality of the Batesford Limestone, on the eastern side of Dog Rocks, in the Australian Portland Cement Company Quarry. Descriptions of the Batesford Limestone have been published by Hall and Pritchard (1892), Chapman (1910), Bowler (1963) and Foster (1970). Ludbrook (1967) indicated an early Miocene age for the deposit.

During the early Miocene, the Dog Rocks pluton existed as a small island which was slowly submerged in a transgressive sea (Bowler 1963). The limestone facies deposited on and adjacent to the island reflect this gradual change, both in lithology (Bowler 1963) and faunal characters (Foster 1970, Chapman 1910). Eleven species of Cirripedia are recorded from several horizons in the Batesford Limestone (Table 1). The distribution is interpreted as being a function of the gradually deepening marine environment. All figured and type material is held by the Palaeontology Section, Bureau of Mineral Resources, Canberra, A.C.T., Australia. RG prefixed numbers refer to the general collections and CPC numbers to type or figured specimens.

SYSTEMATIC PALAEOLOGY

Full descriptions are only given for new taxa. Fuller treatment of other species has been provided by Buckeridge (1982, 1983). Unless otherwise stated, the material was collected by G. Chapronière from the Australian Portland Cement Company Quarry at Batesford, Victoria.

Suborder LEPADOMORPHA Pilsbry 1916

Family SCALPELLIDAE Pilsbry 1907

Genus *Calantica* Gray 1825

Calantica sp. cf. *C. villosa* (Leach 1824)

(Fig. 4e, f)

cf. 1851 *Scalpellum villosum* Leach 1824; Darwin, 274.
cf. 1978 *Calantica villosa* (Leach 1824); Foster, 44-45,
pl. 5E, fig. 26 (see for earlier citations).

MATERIAL: A left scutum, CPC 22589, from sample RG 77640096.

DISTRIBUTION AND AGE: Early Miocene, Victoria; Recent, New Zealand.

DESCRIPTION: Scutum somewhat thickened, strongly reflexed carinally with umbo elevated from valve platform to enclose scutal angle of tergum; growth ridges weak; interior with large deep adductor muscle pit close to apex on occludent margin; basi-tergal angle close to 90°.

REMARKS: This scutum has a more deeply depressed adductor muscle scar than is evident in Recent specimens (a feature that may indicate a more vigorous environment), but otherwise conforms to the New Zealand material (see Foster 1978: 44). *C. villosa* is generally found intertidally, but has been recorded to depths of 201 m off Stephens Is. (Foster 1978).

Genus *Smilium* Leach 1825

Smilium sp. cf. *S. tortachillense* Buckeridge 1983

cf. 1983 *Smilium tortachillense* Buckeridge, 39-40, fig. 28.

MATERIAL: An incomplete right scutum from sample RG 77640091.

DISTRIBUTION AND AGE: For *S. tortachillense*, late Eocene (Aldingan); South Australia.

DESCRIPTION: Apex only slightly inflected carinally; basal margin broadly rounded; exterior without clear apico-basal ridge. Interior with deep, well-formed sub-circular adductor muscle scar positioned slightly above centre.

REMARKS: Poor preservation and lack of diagnostic features prevents a more accurate systematic location of this specimen.

Suborder VERRUCOMORPHA Pilsbry 1916

Family VERRUCIDAE Darwin 1854

Genus *Verruca* Schumacher 1817*Verruca* (*Verruca*) *tasmanica tasmanica* Buckeridge 1983

1983 *Verruca* (*Verruca*) *tasmanica tasmanica* Buckeridge, 57-58, fig. 43.

DIAGNOSIS: Fixed scutum with radioalar wing approximately equitriangular, movable tergum about one and a half times longer than broad.

MATERIAL: Numerous compartments from RG 77640088 and RG 77640089.

DISTRIBUTION AND AGE: Late Cretaceous to early Miocene, Australasia.

REMARKS: Although recent Australasian Verrucidae are known only from depths greater than 250 m (Foster 1978), *Verruca laevigata* is found in the South American littoral zone (Darwin 1854). *Verruca laevigata* is similar to *V. tasmanica*, and it has been proposed by Buckeridge (1983) that an eastward dispersal, from Western Australia, via New Zealand and the Chatham Islands, lead to the establishment of the shallow water South American species.

Suborder BALANOMORPHA Pilsbry 1916

Family PACHYLASMATIDAE Utinomi 1968

REMARKS: Five species of pachylasmatids are recorded from the Batesford Limestone. Of these, *Eolasma rugosa* sp. nov. belongs to an extinct genus, and then only as disarticulated compartments and opercula. With the exception of *Hexelasma* sp. cf. *H. nolearia* Foster, none of the other species have extant representatives. Furthermore, no taxa are known with more than one compartment or valve in intimate association, hence, holotypes have been nominated using compartments, with most likely opercula included within the paratypes.

Subfamily EOLASMINAE Buckeridge 1983

Genus *Eolasma* Buckeridge 1983

DIAGNOSIS: Shell with eight solid calcareous compartments, comprising rostrum, carina and paired latera, carino-latera and rostro-latera; rostro-latera do not enter into sheath; external alar growth lines parallel inferior alar margin; tergum with prominent articular ridge, scutum with weakly elevated articular ridge; basis apparently membranous.

DISTRIBUTION AND AGE: Late Palaeocene to early Eocene: New Zealand; early Miocene: Victoria, Australia.

TYPE SPECIES: *Eolasma maxwelli* Buckeridge 1983 (Late Palaeocene to early Eocene, South and Chatham Islands, New Zealand).

Eolasma rugosa sp. nov.

Figs 1a-k, 2f-h, 3a-d.

DIAGNOSIS: Exterior of compartments strongly rugose, interior with sheath moderate to weakly developed; latera with strongly reflexed alae; tergum with moderately prominent triangular articular ridge, latera depressor muscle crests weakly developed; scutum of low relief.

HOLOTYPE: CPC 20217, a left laterus from RG 77640102, 24.1 m above the basal granitic gravels.

MEASUREMENTS: Holotype, CPC 20217, apico-basal 4.7 mm.

Paratypes:

CPC 20218 rostro-latus

from RG 77640096, apico-basal 6.4 mm

CPC 20219 rostrum

from RG 77640097, apico-basal 8.1 mm

CPC 20220 right carino-latus

from RG 77640096, apico-basal 3.5 mm

CPC 20221 right scutum

from RG 77640097, occludent margin 7.0 mm

CPC 20222 right tergum

from RG 77640097, carinal margin 3.8 mm

CPC 20223 rostro-latus

from RG 77640097, apico-basal 6.1 mm

CPC 22590 carina

from RG 77640097, apico-basal 6.8 mm

CPC 22591 left tergum

from RG 77640099, carinal margin 3.7 mm

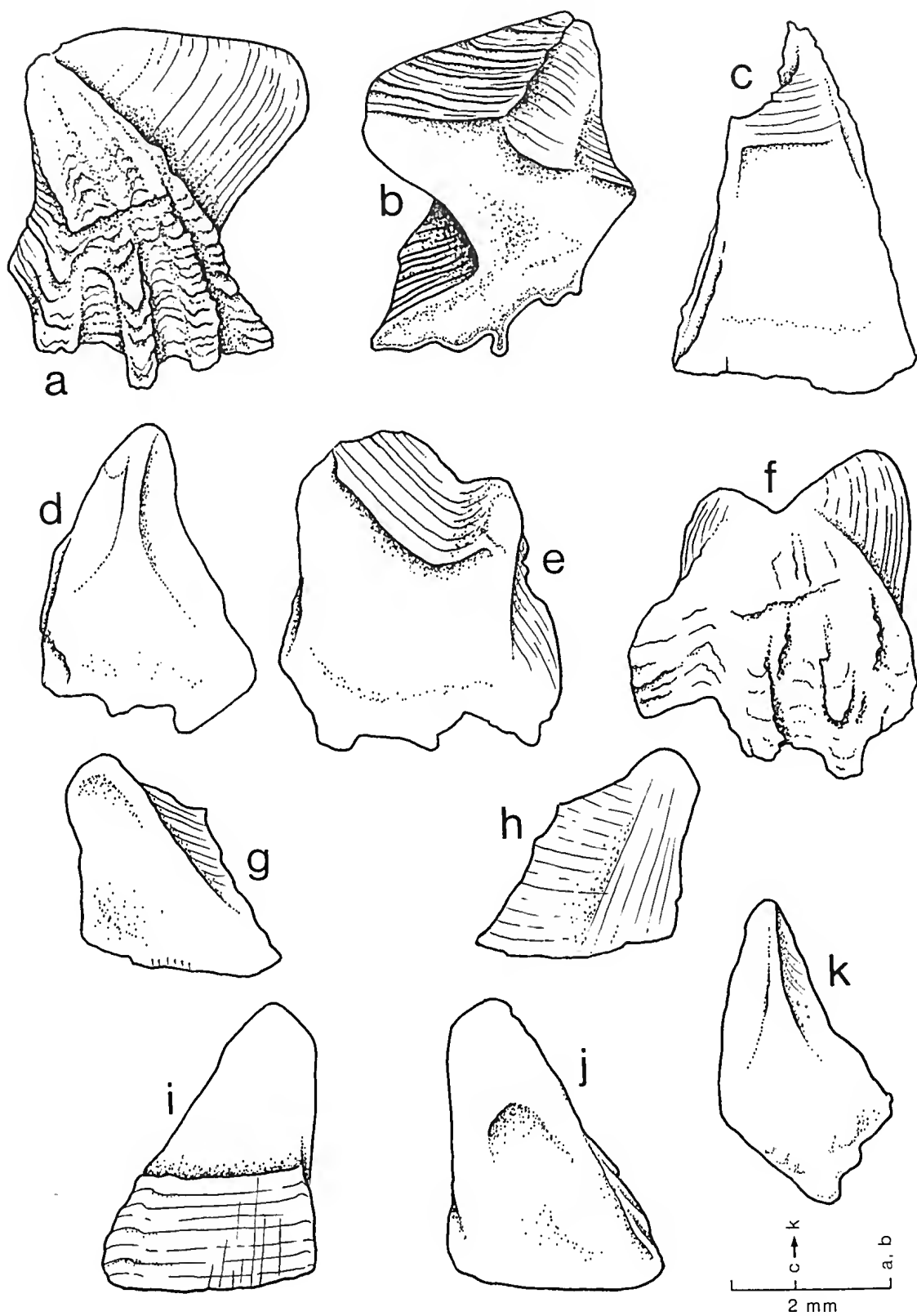
MATERIAL: Numerous disarticulated compartments and valves from the Batesford Limestone A.P.C. Company quarry, Batesford, and the Sherwood Marl, West Head, Flinders.

DISTRIBUTION AND AGE: Early Miocene (Batesfordian), Victoria, Australia.

DESCRIPTION: Compartments solid, calcareous, with coarse, strongly developed longitudinal ribbing, which is cut by sharp growth ridges in some specimens to produce nodes; interior smooth except for fine growth lines on a weak to moderately developed sheath; alae without marginal extensions, growth lines parallel inferior margin, which is broadly rounded at the basal angle; alae often well developed, extending out by about the same width as the paries.

Scutum of low relief, adductor ridge low and broad; adductor muscle scar rounded, moderately deep,

Fig. 1—a-k, *Eolasma rugosa* sp. nov. a, b, left laterus (Holotype), CPC20217, exterior, interior. c, rostrum, CPC20219, interior. d, rostro-latus, CPC20223, interior. e, f, carina, CPC22590, interior, exterior. g, h, right tergum, CPC20222, interior, exterior. i, j, right scutum, CPC20221, exterior, interior. k, rostro-latus, CPC20218, interior.



situated slightly above centre; exterior with fine transverse growth ridges, slightly inflected close to occludent margin and cut by weak to moderately developed longitudinal striae. Tergum sub-triangular, articular ridge rounded ?triangular, moderately prominent; spur at basi-rostral angle; weak crests for lateral depressor muscles; exterior with weak, transverse growth lines cut by apico-basally radiating striae in the central region.

REMARKS: This species is distinguished from *E. maxwelli* by its strong external ribbing and well developed alae. These features effect an articulated shell that is more resistant to erosion than *E. maxwelli*, such that *E. rugosa* may be interpreted as having occupied a more vigorous, and perhaps shallower, environment. This suggestion is further borne out by associated fauna, which includes intertidal barnacles like *Elminius* Leach 1825, and *Tetracitella* Hiro 1939.

ETYMOLOGY: Morphological, alluding to the rugose exterior of the shell (Latin *rugosa* = wrinkled).

Subfamily PACHYLASMATINAE Utinomi 1968

Genus *Pachylasma* Darwin 1854

Pachylasma veteranum Buckeridge 1983

Fig. 2 i,j

1983 *Pachylasma veteranum* Buckeridge, 67-68, fig. 51.

DIAGNOSIS: Compartments considerably thickened, external ribbing either irregular or wanting; sheath weak or wanting; alae with external growth lines parallel to inferior alar margin, with no welting on inner or outer surface of superior alar margin; interior generally smooth, but some weak papillae may develop basally.

MATERIAL: Disarticulated compartments from between RG 77640090 and RG 77640101.

DISTRIBUTION AND AGE: Palaeocene to early Miocene; Australia, Chatham Is.

SUPPLEMENTARY DESCRIPTION: A single right scutum (Fig. 2 i-j) from RG 77640099 does not conform to any of the other stratigraphically-associated cirripeds and may be attributed to *P. veteranum*. It is a typical pachylasmatine scutum with low internal relief and clearly formed apico-basal grooves on the exterior; adductor ridge low, rounded; central portion of interior slightly elevated as a weak adductor ridge; adductor muscle scar weak, elongate, close to occludent margin.

Subfamily BATHYLASMATINAE Newinan & Ross 1971

Genus *Bathylasma* Newman & Ross 1971

DIAGNOSIS: Shell wall of six solid compartments, rostrum not tripartite, rostro-latera absent; external

superior alar margin with welting; terga and scuta generally with prominent articular ridges.

DISTRIBUTION AND AGE: Palaeocene to Recent. Palaeocene, Chatham Is; Oligocene, New Zealand; Miocene to Recent, New Zealand, Victoria; Recent, deep seas.

TYPE SPECIES: *Balanus corolliformis* Hoek 1883. Pleistocene to Recent. Circum-Antarctic.

Bathylasma costatum sp. nov.

Figs 2a-e, 3g, h, 4g-j

DIAGNOSIS: Compartments moderately thick with strong, sharply defined longitudinal ribs separated by slightly more than their own width; alae with external growth lines diverging from inferior alar margin, superior alar margin with a moderate to weak welting; interior with very weak longitudinal ribbing; sheath poorly developed.

HOLOTYPE: CPC 22583, a rostrum from RG 77640106, 30.8 m above basal granitic gravels.

MEASUREMENTS: Holotype, CPC 22583, apico-basal 4.6 mm.

Paratypes:

CPC 22584 left latus

from RG 77640106, apico-basal 3.6 mm

CPC 22585 rostrum

from RG 77640106, apico-basal 4.9 mm

CPC 22586 carina

from RG 77640106, apico-basal 4.4 mm

CPC 22587 right scutum

from RG 77640099, occludent margin 5.4 mm

CPC 22588 left tergum*

from RG 77640107, carinal margin 7.5 mm

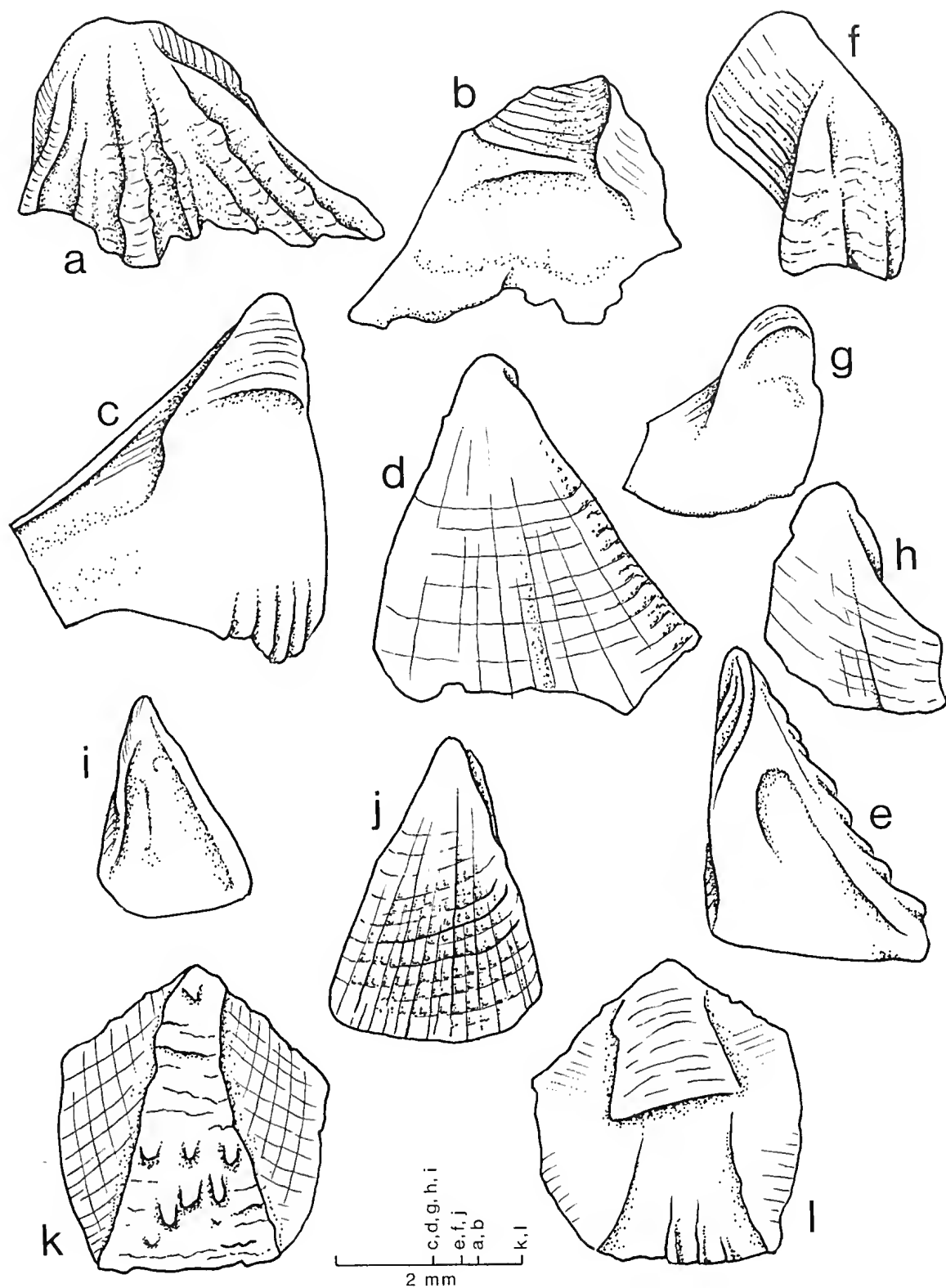
*denotes incomplete valve.

MATERIAL: Numerous disarticulated compartments, principally from horizons 25.6 m or more above the basal granitic gravels. Disarticulated compartments from the Sherwood Marl, RG 77640066 and RG 77640067 (cliff behind shore platform at West Head, Flinders).

DISTRIBUTION AND AGE: Early Miocene (Batesfordian), Victoria, Australia.

DESCRIPTION: Shell moderately low, conical; compartments solid, moderately thick with strong, sharply defined, non-bifurcating longitudinal ribs, each separated by a little more than its own width; alae with external growth lines diverging from inferior alar margin, superior alar margin with a moderately developed welting; interior with very weak longitudinal ribbing or

Fig. 2—a-e, *Bathylasma costatum* sp. nov. a, b, left latus, CPC22585, exterior, interior. c, d, left tergum, CPC22588, interior, exterior. e, right scutum, CPC22587, interior. f-h, *Eolasma rugosa* sp. nov. f, right carino latus, CPC20220, exterior. g, h, left tergum CPC22591, interior, exterior. i, j, *Pachylasma veteranum* Buckeridge, right scutum (ex RG77640099), interior, exterior. k, l, *Acasta* sp. cf. *A. cyathus* Darwin, rostrum, CPC22582, exterior, interior.



weak basal papillae; sheath poorly developed, especially on carinae; basis wanting.

REMARKS: The assignation of opercular valves to this species is tentative. Three other pachylasmatids are known to have co-existed with this species, and whilst opercula of *Eolasma* are distinctive, the differences between those of *Hexelasma* sp. cf. *H. nolearia*, *B. costatum* and *P. veteranum* are not clear. One mitigating circumstance is that although the known stratigraphic range of *Hexelasma* sp. cf. *H. nolearia* and *P. veteranum* is much greater than *B. costatum*, these opercula are found only in *B. costatum* horizons. However, difficulties clearly remain, particularly with respect to the relatively large size of the tergum (CPC 22588), which would have belonged to a much bigger shell than present reconstructions suggest. *Note:* Without these opercula, the small size and relatively thick compartments of *B. costatum* could be included within *Mesolasma*.

Tergum (CPC 22588) moderately elongate, articular ridge moderately high, triangular; lateral depressor muscle crests well developed; exterior with shallow, concave furrow; growth lines slightly inflected on occludent margin; faint apico-basal striae radiate from the apex to the basal margin in the carinal half. A further tergum, very incomplete and partially decorticated, from RG 77640106 differs from CPC 22588 in having no clear articular ridge. This difference may be ontogenetic, as other features conform. Scutum (CPC 22587) with articular ridge relatively low; adductor ridge weak, broadly rounded; adductor muscle scar moderately shallow, central; exterior with fine transverse growth lines.

ETYMOLOGY: Morphological, alluding to the ribbed exterior of the compartments (Latin *costa* = a rib).

Genus *Mesolasma* Foster 1981

?*Mesolasma newmani* Buckeridge 1983

Fig. 3e, f

1983 ?*Mesolasma newmani* Buckeridge, 70-71, fig. 53.

DIAGNOSIS: Compartments thickened, with weak longitudinal external ribbing; sheath well formed; interior with fine weak ribs basally; base of paries broad, flat, with numerous fine grooves and papillae.

MATERIAL: Disarticulated compartments from RG 77640090 to 77640094.

DISTRIBUTION AND AGE: Oligocene to Miocene (Janjukian to Batesfordian), Victoria, Australia.

REMARKS: Although very similar to that described by Buckeridge (1983) from the Point Addis Limestone, this material shows a higher degree of abrasion and decoration. Further, the alar development is greater in some compartments, suggesting that this extension may have

been developed in mitigation of a more energetic environment.

Subfamily HEXELASMINAE Newman & Ross 1976

Genus *Hexelasma* Hoek 1913

Hexelasma sp. cf. *H. nolearia* (Foster)

Figs 3i-l, 4c, d

1983 *Hexelasma* sp. cf. *H. nolearia* (Foster 1978); Buckeridge, 71, fig. 54.

DIAGNOSIS: Compartments externally with distinct growth ridges; parietes divided into thicker outer and thinner inner shell laminae; internal ribbing low, terminating as papillae on the basal margin.

MATERIAL: Disarticulated compartments from RG 77640086-77640107, RG 77640123-77640126, Batesford Limestone, A.P.C. Company Quarry, Batesford. RG 77640066-77640068, Sherwood Marl (Batesfordian), Flinders. RG 77640184, Fishing Point Marl (Longfordian), Hordern Vale. Collected by G. Chapronière in 1977. RG 77640111, Fyansford Formation (Bairnsdalian), Torquay. Collected by S. Shafik in 1977.

DISTRIBUTION AND AGE: Longfordian to Bairnsdalian (early to middle Miocene), Victoria, Australia.

REMARKS: An isolated scutum (CPC 25611) from RG 77640087 is likely to belong to this species. It is somewhat apico-basally elongated and possesses an adductor ridge, much like that of *Hexelasma nolearia*; it has a moderately low articular margin, but unlike *H. nolearia* is relatively thick. This last feature may be an environmental adaptation, but without further material, no firm conclusions can be drawn.

Family TETRACLITIDAE Gruvel 1903

Subfamily TETRACLITELLINAE Newman & Ross 1976

Genus *Tetraclitella* Hiro 1939

?*Tetraclitella* sp. cf. *T. purpurascens* (Wood)

Fig. 4a, b.

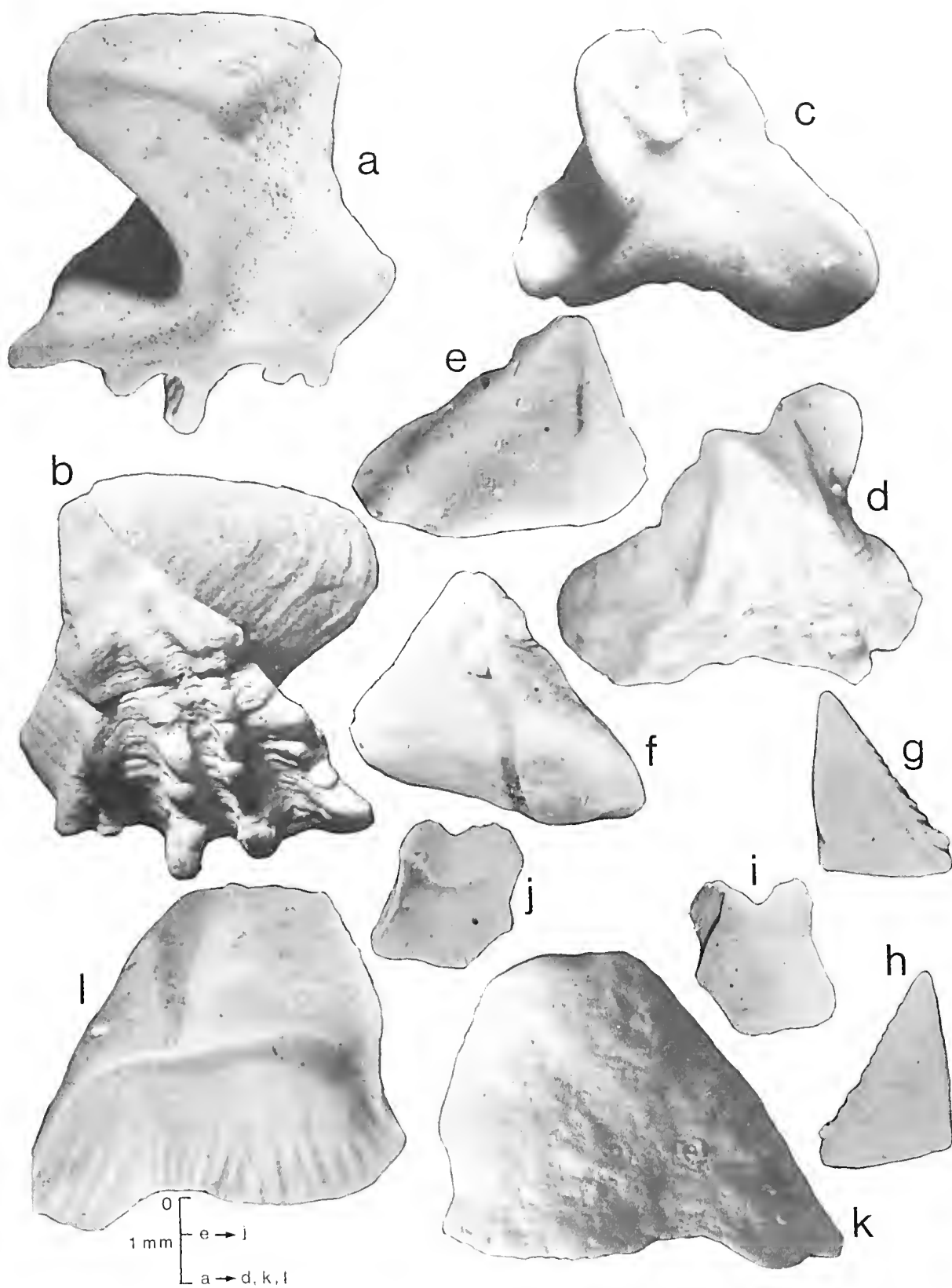
cf. 1983 *Tetraclitella* sp. cf. *T. purpurascens* (Wood 1915); Buckeridge, 77-78, pl. 5c, d.

MATERIAL: Two articulated compartments from RG 77640091 (Fig. 4a, b), isolated compartments from RG 77640090, RG 77640095, RG 77640099.

DISTRIBUTION AND AGE: Early Miocene (Batesfordian), Victoria, Australia.

DESCRIPTION: Shell low, flat; parietes with a large number of small rounded hexagonal tubes; sheath weak, non-pendant; exterior with 30 or more fine, distinct, apico-basal ribs; radii smooth, sunken; internal nature of radii unknown, operculum unknown.

Fig. 3—a-d, *Eolasma rugosa* sp. nov. a, b, left latus (Holotype), CPC20217, interior, exterior. c, d, left latus (ex RG77640096), interior, exterior. e, f, ?*Mesolasma newmani* Buckeridge, right carino-latus (ex RG77640097), interior, exterior. g, h, *Bathylasma costatum* sp. nov. right scutum, CPC22587, interior, exterior. i-l, *Hexelasma* sp. cf. *H. nolearia* Foster. i, j, carina (ex RG77640090), exterior, interior. k, l, latus (ex RG77640102), exterior, interior.



REMARKS: This material is too poorly preserved to permit a more accurate taxonomic location. The best specimen is made up of two remarkably well-fused compartments, one of which was probably a latus. Unfortunately, the outer margins of both compartments are so corroded that the structure of the abutment areas of both parietes and radii is indeterminate. However, a radius is developed between the two compartments; this is sunken below the surface and is likely to have possessed a horizontal summit. The radius appears relatively smooth and very thin, the pores (if they are present at all) would probably be very small. The only clear way to determine the exact nature of the radii would be to break the specimen, but as the material is brittle, this course of action has not yet been pursued. The morphology of the compartments suggests a very low, flat shell, with perhaps 30 fine, distinct apico-basal ribs separated by their own width. Internally, the compartments can be seen to be comprised of a very large number of small tubes; the sheath is weakly formed and is not pendant. This material probably represents a new species, and can be distinguished from other Australasian *Tetracitella* by the large number of external ribs. Further material with radii and hopefully, opercula, should clarify the status of these specimens.

Family ARCHAEOBALANIDAE Newman & Ross 1976

Subfamily ARCHAEOBALANINAE Newman & Ross 1976

Genus *Acasta* Leach 1817

Acasta cyathus Darwin 1854

1854 *Acasta cyathus* Darwin, 312, pl. 9, figs 3a-3c.

DIAGNOSIS: Carino-lateral parietes about quarter the width of lateral parietes; radii wider than parietes; basis nearly flat; tergum with spur truncated, half as wide as valve.

DISTRIBUTION AND AGE: ?Miocene, Victoria; Recent, Morocco, Caribbean, East Africa, Indian Ocean.

Acasta sp. cf. *A. cyathus* Darwin 1854

Fig. 2k, l

MATERIAL: CPC 22582, a rostrum from RG 77640097, incomplete compartments from between RG 77640097 and RG 77640100.

REMARKS: Although this material appears to belong to extant *A. cyathus*, a more definite taxonomic location cannot be made without articulated compartments and opercula. *A. cyathus* is characteristic of moderately deepwater conditions, recent species being found between 15-180 m.

Subfamily ELMINIINAE Foster 1982

Genus *Elminius* Leach 1925

Elminius (Matellionius) chapronierei Buckeridge, 1982

1982 *Elminius (Matellionius) chapronierei* Buckeridge, 353-357, figs 1, 2, 3

DIAGNOSIS: Compartments with a thickened, inflected, inner basal margin, scutum with articular ridge low, rounded, not dependent basally; tergum with spur confluent with basi-rostral angle.

MATERIAL: CPC 20213, holotype, complete shell with opereulum; numerous compartments from RG 77640086-77640096.

DISTRIBUTION AND AGE: Early Miocene (Batesfordian), Victoria.

REMARKS: *Elminius chapronierei* is the oldest known species of *Elminius* from Australia. The thickening of the basal margin is a unique feature amongst the Elminiinae and is interpreted as an attempt at strengthening the shell to offset the effects of a vigorous environment. The species shows a similarity with *Palaeobalanus linsayi* Buckeridge 1983, from the Aldingan of South Australia, thus emphasising the link between the Archaeobalaninae and the Elminiinae (Buckeridge 1982).

Further archaeobalanid remains have been recovered from RG 77640184 (Longfordian Age; Fishing Point Marl, Lake Horden, Victoria; collected by G. Chapronière in 1977) and RG 77640111 (Bairnsdalian Age; Fyansford Marl, Batesford; Collected by S. Shafik in 1977). Unfortunately insufficient material is available for an accurate taxonomic location to be made. The material, unlike *E. chapronierei*, possesses broad radii, and, unlike *A. cyathus*, has wide parietes; growth form indicates that this material probably grew on a substrate similar to echinoderm spines.

CIRRIPED DISTRIBUTION IN THE BATESFORD LIMESTONE

Although the balanomorph barnacles are well represented in the Batesford Limestone (Table 1), a significant aspect is the absence from the fauna of the Chthamaloidea. Present Australian shores are inhabited by a diverse range of chthamaloids (e.g. *Catomerus* Pilsbry 1916, *Chamaesipho* Darwin 1854, *Chthamalus* Ranzani 1817, *Euraphia* Conrad 1837, *Octomeris* Sowerby 1825), and whilst these are characteristic of the upper littoral zone, those with thicker plates could be expected to contribute to the loose shell material collecting immediately offshore. Fossil chthamaloids are rare and, except for *Pachydiadema* from the Cretaceous, are known only from a few horizons (i.e. *Chthamalus* from the Miocene of Chile and Pliocene of Italy, *Chamaesipho* from the early Miocene of New Zealand). This poor fossil record reflects the high energy (highly corrosive) upper littoral environment occupied by chthamaloids, an environment that is rarely preserved intact except under conditions of rapid subsidence and burial. However, the

Fig. 4—a, b, ?*Tetracitella* sp. cf. *T. purpurascens* (Wood) ?rostrum and latus (ex RG77640091), exterior, interior. c, d, *Hexelasma* sp. cf. *H. nolearia* Foster rostrum (ex RG77640098), interior, exterior. e, f, *Calantica* sp. cf. *C. villosa* (Leach) left scutum, CPC22589, exterior, interior. g-j, *Bathylasma costatum* sp. nov. g, h, rostrum (Holotype), CPC22583, exterior, interior. i, j, left latus, CPC22584, interior, exterior.

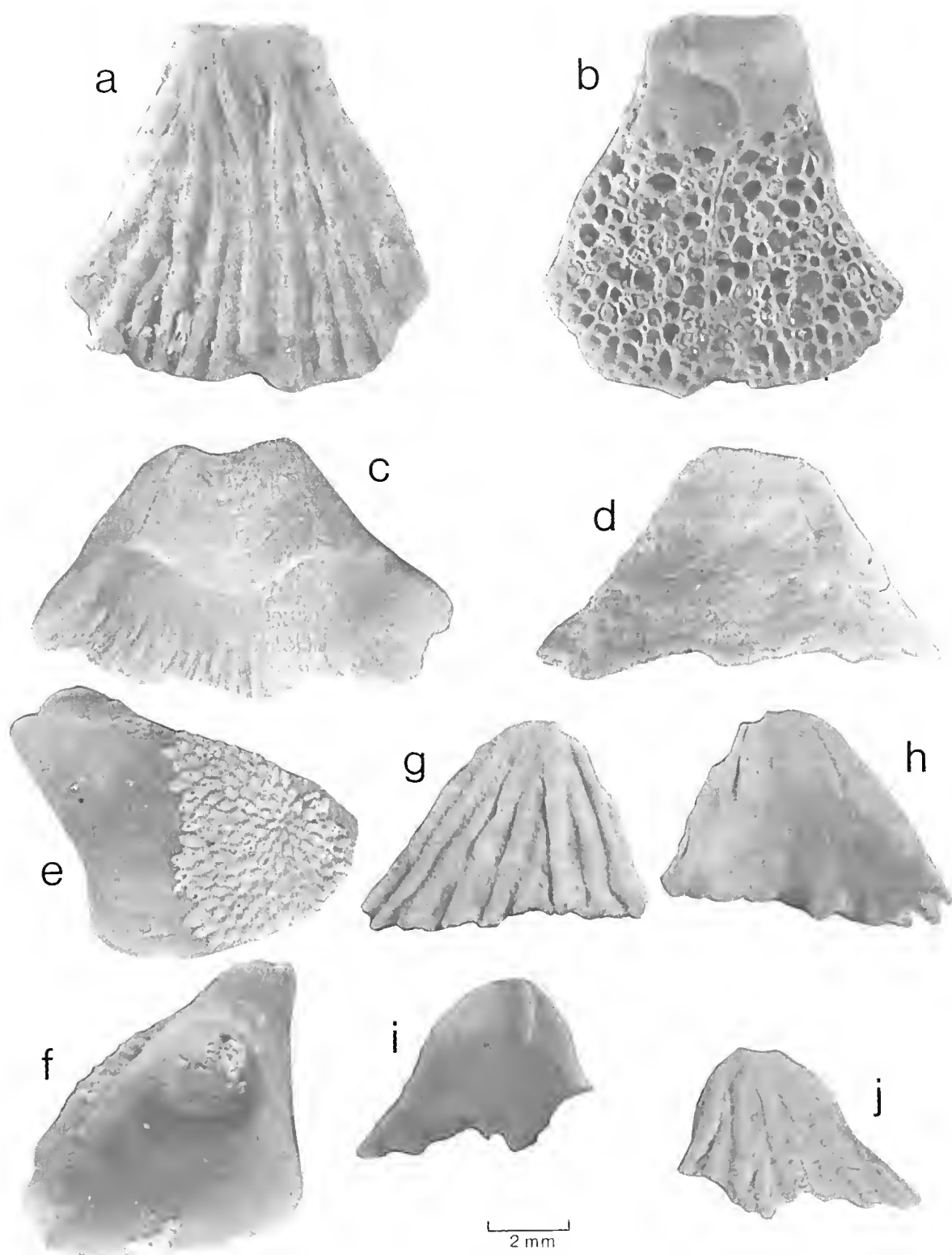


TABLE 1

DISTRIBUTION OF BARNACLES IN A STRATIGRAPHIC SEQUENCE TAKEN FROM THE QUARRY FACE, 245 DEGREES NORTH FROM THE QUARRY OFFICE, AUSTRALIAN PORTLAND CEMENT COMPANY QUARRY, BATESFORD, IN 1977. † INDICATES OCCURRENCE; * INDICATES PROBABLE OCCURRENCE.

Collection Number	<i>Elninius clapronierei</i>	<i>Tetractiella</i> sp. cf. <i>T. purpurascens</i>	<i>Smilium</i> sp. cf. <i>S. tortachillense</i>	<i>Acasta</i> sp. cf. <i>A. cyathus</i>	<i>Verruca tasmanica</i>	? <i>Mesolasma newmani</i>	<i>Pachylasma veteranum</i>	<i>Calanica</i> sp. cf. <i>C. villosa</i>	<i>Hexelasma</i> sp. cf. <i>H. nolearia</i>	<i>Eolasma rugosa</i>	<i>Bathylasma costata</i>	Height Above Quarry Floor (m)
RG 77640086	†								*			0
RG 77640087	†								†	?		3.0
RG 77640088	†				†							4.6
RG 77640089	†				†				†			6.7
RG 77640090		†				?			†	†		8.2
RG 77640091		†	†			†	†			†		9.8
RG 77640092										†		11.0
RG 77640093						†	†		†	†		12.5
RG 77640094						†			†	†		14.6
RG 77640095		*								†		15.9
RG 77640096	*						†	†	†	†	†	17.1
RG 77640097				†		†	†		†	†		18.3
RG 77640098				†	*		†		†	†		19.5
RG 77640099		*				†			†	†	†	21.0
RG 77640100				†					†	†		22.3
RG 77640101							†		†	†		23.5
RG 77640102									†	†		24.1
RG 77640103									†	†	†	25.6
RG 77640104									†	†	†	26.5
RG 77640105									†	†	†	29.6
RG 77640106							?		†	†	†	30.8
RG 77640107					†				†		†	32.6

TABLE 2
STRATIGRAPHIC DIVISIONS IN THE BATESFORD LIMESTONE, SHOWING TAXA CHARACTERISTIC OF EACH ZONE
AND LIKELY SOURCE ENVIRONMENT.

Zone	Height Above Basal Gravels (m)	Sample Range	Significant Taxa	Likely Provenance
A	0-6.7	77640086-089	<i>Elminius</i> <i>Verruca</i>	littoral
B	0.2-22.3	77640090-100	? <i>Tetrachitella</i> <i>Acasta</i> <i>Calantica</i> ? <i>Mesolasma</i>	upper sublittoral
C	23.5-32.6	77640101-107	<i>Bathylasma</i>	sublittoral (cooler?)

non-preservation of the chthamaloïds in the Batesford Limestone is not altogether a satisfactory explanation for their absence, as other littoral taxa (*Elminius*, ?*Tetrachitella*) are present. Rather, their absence could suggest that the environment was locally unsuitable for chthamaloïds, or that no chthamaloïds occurred in the region. The distribution of modern chthamaloïds is governed by pressures such as competition and predation; but it appears that competition, at least from barnacles, would have been less during this period, as the highly successful balanines are not known from the Australasian lower Miocene.

It appears likely that both chthamaloïds and balanines were introduced into the area from the Indo-Malayan region during the upper Miocene and Pliocene, but further collecting will be required to accurately pinpoint the source and arrival time of these taxa.

VERTICAL DISTRIBUTION

The gradual and apparently continuous increase in water depths at Dog Rocks has provided a valuable record of the relative water depths that were inhabited by barnacles. The collection numbers 77640086 to 77640107 comprise a stratigraphic sequence up the quarry face to a height of 32.6 m from the quarry floor. The lithological changes in the sequence, from calcareous 'basal' granitic sands and gravels through to a shallow water calcarenite (see Bowler 1963) are reflected in the vertical change in the composition of the barnacle population (Table 1). This sequence can be conveniently divided into three parts, each with a characteristic suite of barnacles indicative of a particular environment (Table 2).

Dr. G. Chapronière (pers. comm.) has indicated that as well as an increase in depth, foraminiferal evidence suggests a gradual cooling, a feature which may further emphasise the barnacle zonations.

COMPARISONS WITH RECENT DISTRIBUTION

The most significant difference lies in the shallow

water occurrences of the verrucids and pachylasmoids, which in present day Australian conditions are deep water taxa. Barnacles are an opportunistic group, quickly adapting to fill available niches, and during the early Palaeogene (when balanines had not yet evolved), pachylasmoids occupied favourable shallow water conditions (Buckeridge 1983). This distribution was to change later in the Cenozoic as the evolving balanines, with a more efficient metabolism, smothered and out-competed other shallow water barnacles. However, the influx of balanines at Dog Rocks seems to have occurred a little later than in other regions (e.g. New Zealand, Italy), enabling the pachylasmoids to survive in their shallow water habitats. Indeed, the Batesford Limestone contains the youngest known *Eolasma*, which in neighbouring New Zealand, survived only to the Eocene (Buckeridge 1983). The verrucids also are normally restricted to deeper waters but there are still a few species that have managed to survive in the highly competitive littoral zone (*Verruca laevigata* Darwin 1854, of Chile and *V. stroemia* Muller 1776, of Europe).

Of the taxa present, perhaps two have extant records (*Acasta*, ?*Tetrachitella*). Amongst the others, only deductions can be made as to their preferred environments, but it seems probable that *Elminius* was littoral, especially as extant *Elminius* is littoral and the only other fossil *Elminius* is from an estuarine environment in the New Zealand Oligocene (Buckeridge 1984). Some interpretation may be placed on shell morphology, with those species that are characterised by thick, robust, often distorted compartments, being characteristic of high energy zones. This morphology is evident in *Eolasma rugosa* and *Pachylasma veteranum*, both of which are here interpreted as upper sublittoral. There are some discrepancies (e.g. *Hexelasma* sp. cf. *H. nolearia*, a relatively thin-walled and, externally, smooth-shelled species), but it is possible that these taxa could have occupied a less vigorous micro-environment in the sublittoral.

ACKNOWLEDGEMENTS

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FOOD OF INTRODUCED MAMMALIAN PREDATORS IN TWO VICTORIAN NATIONAL PARKS

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ABSTRACT: The diets of introduced mammalian predators (foxes, dogs and cats) living in the Little Desert and Wyperfeld National Parks in north-western Victoria were studied by scat analysis to determine the extent of predation on native fauna. Food items included mammals, birds, reptiles, insects and other invertebrates, and plant material. Mammals appeared to be the most important food items with exotic species (*Oryctolagus cuniculus* and *Mus musculus*) occurring much more frequently than indigenous species. Only two (*Macropus fuliginosus* and *Trichosurus vulpecula*) of the 11 species of indigenous terrestrial mammals known to occur in the Parks made any significant contribution to the diet of the predators. Predation on birds and reptiles was generally low and, while insect and plant remains occurred frequently, the number of scats containing large quantities of either was low.

Studies such as that of Triggs, Brunner and Cullen (1984) on the diets of introduced mammalian predators (foxes, *Vulpes vulpes*; dogs, *Canis familiaris*; and, cats, *Felis catus*) have shown that they prey on both introduced and indigenous mammals, and a wide variety of other indigenous wildlife. Plant material is also eaten. The conclusion reached in most studies (e.g. McIntosh 1963, Coman & Brunner 1972, Croft & Hone 1978, Jones & Coman 1981, Woolley & Valente 1982) is that they are opportunistic predators and scavengers, feeding on whatever is abundant and easily available at the time. Thus in agricultural areas domestic stock (eaten mostly as carrion) may form a major component of the diet (McIntosh 1963, Coman 1973); whereas in areas containing no domestic stock introduced mammals such as the rabbit, *Oryctolagus cuniculus*, and the feral house mouse, *Mus musculus*, may form major components (Ryan & Croft 1974, Seebeck 1978). In bush areas where there are few rabbits or mice indigenous mammals may form an important component of the diet (Coman & Brunner 1972, Brunner, Lloyd & Coman 1975, Triggs *et al.* 1984). Control of introduced mammalian predators may therefore, depending on the availability of other foods, be desirable in National Parks to protect native fauna.

Following a suggestion by the Research Co-ordinator of the National Parks Service of the Department of Conservation, Forests and Lands, a study of the diet of introduced mammalian predators in the Little Desert and Wyperfeld National Parks was carried out to determine the extent of predation on native fauna. Diet was investigated by analysis of remains in scats. Foxes and feral dogs and cats are known to occur in both Parks.

STUDY AREAS

The Little Desert National Park (area 35,240 ha), in the heart of Victoria's wheat growing Wimmera district, was originally set aside to protect the Mallee Fowl. Predator scats were collected in the three most extensive

vegetation types within the Park, viz. heathland, broombush shrubland and riverain woodland (Cheal, Day & Meredith 1979, Fig. 27), and in Crown Land adjoining the northern boundary of the Park.

Wyperfeld National Park (area 100,000 ha) was reserved to protect an area of typical mallee country. Scats were collected in heathland, mallee shrubland and riverain woodland, these being the most extensive vegetation types within the Park (Cheal *et al.* 1979, Fig. 28).

Scats were collected on walking tracks and roads in one or more areas within each vegetation type in each Park. The collecting localities are shown in Fig. 1 (Little Desert National Park) and Fig. 2 (Wyperfeld National Park). In each locality collections were made from 26 February to 5 March, 30 April to 3 May and 9 to 13 July 1979.

SCAT ANALYSIS

Each scat, or group of scats from a single dropping, was placed in a labelled envelope and oven-dried at 80°C for 48 hours to destroy the eggs of parasites. The scats were soaked individually in water for up to 48 hours to soften them. They were then broken up, poured into a 248 µm aperture sieve and washed. The remaining material was placed in a white enamel tray and sorted into the following categories: hair, feathers, scales, teeth, bones, egg shell, invertebrates and material of plant origin. The components were dried and, as far as possible, identified.

Hair was identified using the method described by Brunner and Coman (1974). Samples of hair from all species of terrestrial mammals known to occur in the Parks (Cheal *et al.* 1979, Table 32) were obtained from Museum collections and a reference collection of cross sections, whole mounts and scale casts of the hair of each species prepared. Hairs from the scats were identified by comparison with both the reference collection and the photographs in Brunner and Coman (1974).

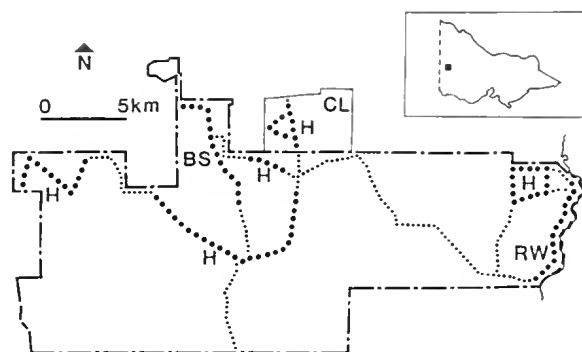


Fig. 1—The collecting localities in heathland (H), broombush shrubland (BS) and riverain woodland (RW) in Little Desert National Park. CL = Crown Land.

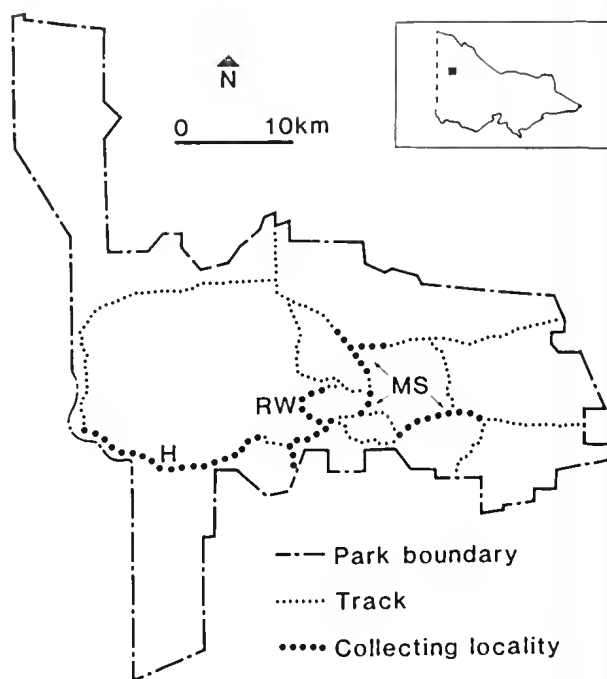


Fig. 2—The collecting localities in heathland (H), mallee shrubland (MS) and riverain woodland (RW) in Wyperfeld National Park.

RESULTS

A total of 923 scats was collected in the Little Desert National Park (LDNP) and 882 in Wyperfeld National Park (WNP). Similar numbers were obtained in each collecting period in each Park. Most were judged, on the basis of appearance and/or odour, to be from foxes. Fox scats have a characteristic 'tail', formed by the drawing out of one or both ends of the scat (Burrows 1968), and fresh ones have a characteristic odour. Only 16 scats, collected in LDNP, were considered to be of cat origin. The possibility exists that some of the smaller 'fox' scats were from cats. Less than 1.5% of the scats collected in each Park (16 in LDNP, 11 in WNP) were considered, largely on the basis of size, to be from dogs. The number of scats in which each of six categories of food items were found, and the frequency of occurrence of these items in the total sample from each Park, are shown in Table 1.

The remains found most frequently in scats were of mammalian origin and consisted of either hair or bone or both. Of the scats containing mammal remains, 577 of 599 collected in LDNP and 537 of 650 collected in WNP contained hair and/or bones which permitted

identification of the species caught. Some scats contained the hair of more than one species. Most bone samples consisted of small pieces which were unsuitable for specific identification, but occasionally jaw bones, teeth and claws, which could be identified, were present. The frequency of occurrence of mammal species identified in scats is shown in Table 2. Bird remains consisted mostly of small pieces of egg shell and feathers, the barbs and barbules of which had been destroyed in the digestive processes; they could not be further identified. Reptile remains included skin, scales, bones, claws and an egg. The species recognised in scats from LDNP included *Varanus* sp., *Amphibolurus* sp., *Ctenotus* sp.,

TABLE 1
PERCENTAGE OCCURRENCE OF FOOD ITEMS IN SCATS COLLECTED IN THE LITTLE DESERT (LDNP) AND WYPERFELD (WNP) NATIONAL PARKS. N = NUMBER OF SCATS IN WHICH FOOD ITEM WAS FOUND.

Food items	LDNP		WNP	
	N	%	N	%
Mammals	599	64.9	650	73.7
Birds	135	14.6	42	4.9
Reptiles	26	2.8	33	3.7
Insects	346	37.5	363	41.2
Other invertebrates	35	3.8	3	0.3
Plant material	574	62.2	344	39.0
Total number of scats	923		882	

TABLE 2
PERCENTAGE OCCURRENCE OF REMAINS OF EXOTIC AND INDIGENOUS MAMMALS IN SCATS COLLECTED IN THE LITTLE DESERT (LDNP) AND WYPERFELD (WNP) NATIONAL PARKS. N=NUMBER OF SCATS IN WHICH SPECIES WAS FOUND.

Mammalian species	LDNP		WNP	
	N	%	N	%
EXOTIC				
<i>Oryctolagus cuniculus</i>	179	31.0	244	45.4
<i>Mus musculus</i>	133	23.0	147	27.4
<i>Ovis aries</i>	164	28.4	6	1.1
<i>Capra hircus</i>	3	0.5	0	0
<i>Felis catus</i>	7	1.2	0	0
<i>Vulpes vulpes</i>	5	0.9	0	0
<i>Canis familiaris</i>	2	0.3	0	0
INDIGENOUS				
<i>Macropus fuliginosus</i>	90	15.6	66	12.3
<i>Trichosurus vulpecula</i>	65	11.3	60	11.2
<i>Sminthopsis crassicaudata</i>	8	1.4	0	0
<i>Anechinus flavipes</i>	2	0.3	0	0
<i>Ningau</i> sp.	0	0	1	0.2
<i>Pseudomys apodemoides</i>	11	1.9	27	5.0
<i>Notomys mitchelli</i>	9	1.6	6	1.1
<i>Tachyglossus aculeatus</i>	4	0.7	5	0.9
Total number of scats containing identifiable mammalian remains.	577		537	

Phyllodactylus marmoratus and *Tiliqua rugosa*. In seats from WNP *Varanus gouldii*, *Amphibohurus* sp., *Ctenotus* sp., *Tiliqua rugosa*, *Chelodina longicollis* and a juvenile of *Pseudonaja textilis* were found.

Identifiable insect remains were found in 180 of 346 seats from LDNP, and 293 of 363 from WNP. Many seats from both Parks contained only very small amounts of insect material; in LDNP insects made up a substantial part of the seat in only 33 instances and in WNP, only 46 contained no other food items. The orders and families of insects represented, and the number of seats in which they were found, are shown in Table 3. The most commonly occurring insects were carabids and tenebrionids in LDNP, and blattids, tenebrionids and gryllids in WNP. Invertebrates other than insects occurred infrequently and included spiders, scorpions and centipedes.

Plant material, including twigs, leaves, grass, fruit and seeds, was found frequently in seats but often in only small amounts, especially in LDNP. There, only 57 of the 574 seats containing plant material included a large amount, and identifiable remains were found in only 73 seats. In WNP 309 of 344 seats contained identifiable plant material, 149 with large quantities. The plant species identified, and the number of seats in which they were found, are shown in Table 4. The most commonly occurring species were *Gyrostemon australasicus* in LDNP seats, and *Solanum simile* and *Billardiera cymosa*, in WNP seats.

Seats were collected in each of three periods (between late February and mid-July) and three vegetation types in

TABLE 3
THE OCCURRENCE OF INSECT REMAINS IN SCATS COLLECTED IN THE LITTLE DESERT (LDNP) AND WYPERFELD (WNP) NATIONAL PARKS.

Insects	Number of seats	
	LDNP	WNP
O. Coleoptera		
F. Carabidae	97	11
Tenebrionidae	46	59
Cerambycidae	3	0
Cantharidae	1	13
Histeridae	1	1
Silphidae	1	10
Scarabaeidae	0	24
O. Orthoptera		
F. Tettigoniidae	21	0
Gryllotalpidae	6	19
Gryllidae	1	59
O. Hymenoptera		
F. Formicidae	2	0
O. Dermaptera		
F. Forficulidae	2	0
O. Diptera		
F. Tachinidae	13	0
O. Hemiptera		
F. Reduviidae	0	1
O. Mantodea	1	7
O. Blattodea	0	137
O. Odonata	2	0
O. Lepidoptera	2	0
O. Isoptera	1	0

TABLE 4

THE OCCURRENCE OF PLANT MATERIAL IN SCATS COLLECTED IN THE LITTLE DESERT (LDNP) AND WYPERFELD (WNP) NATIONAL PARKS.

Plants	Number of scats	
	LDNP	WNP
<i>Gyrostemon australasicus</i>	30	2
<i>Leucopogon cordifolius</i>	9	5
<i>Leptospermum myrsinoides</i>	9	0
<i>juniperinum</i>	2	0
<i>coriaceum</i>	0	2
<i>Medicago minima</i>	4	4
<i>Astroloma conostephioides</i>	2	0
<i>Eucalyptus leucoxylon</i>	1	0
<i>camaldulensis</i>	1	1
<i>baxteri</i>	6	0
<i>largiflorens</i>	0	1
<i>incrassata</i>	0	1
sp.	0	8
<i>Casuarina paludosa</i>	2	0
<i>luhmännii</i>	0	4
<i>Lepidobolus drapetocoleus</i>	1	0
<i>Hibbertia stricta</i>	1	0
<i>Solanum simile</i>	0	188
<i>Bromus</i> sp.	1	7
<i>Danthonia</i> sp.	0	1
<i>Triticum aestivum</i>	3	0
<i>Hordeum</i> sp.	4	0
<i>Billardiera cymosa</i>	0	119

the two Parks. A full seasonal comparison cannot be made, and it is not known if the scats collected in each vegetation type contained only food items eaten there, but little variation in the occurrence of various categories of food items was evident. The variations that were seen were consistent with expected seasonal changes in the abundance of the particular species or with known habitat preferences. For example, insect and reptile remains were less frequent in scats collected in winter (July) than in the two earlier collections; and the remains of *Trichosurus vulpecula*, a species largely dependent on trees for nest sites, were found most commonly in scats collected in riverain woodland. An increase in remains of *Mus musculus* in the third collection from WNP coincided with the beginning of a mouse plague (I. Norman pers. comm.).

DISCUSSION

Although it was not possible to determine with certainty the specific origin of the predator scats collected in this study, we consider that the majority were from foxes and that the results of scat analysis largely reflect the foods eaten by this predator. The range of food items found in the scats, and the percentage occurrence of each category, are in general accord with the results of studies on the diet of foxes carried out by others (e.g. McIntosh 1963, Coman 1973, Brunner *et al.* 1975). The most frequently occurring items found in the scats were the remains of mammals, insects and plants, with more

scats containing mammal remains than other items. Mammals probably constitute the major food item, as the total number of scats containing large quantities of either insect or plant material was low. Birds (except in LDNP), reptiles and invertebrates other than insects occurred infrequently.

The mammalian remains found most frequently in scats were those of exotic species, in particular the rabbit (*Oryctolagus cuniculus*) and the house mouse (*Mus musculus*) both of which are known to occur commonly in the two Parks. The remains of sheep (*Ovis aries*), which occur in high densities around the Park, were also commonly found in scats from LDNP. Sheep may wander into the Park, or predators may move out to feed. Sheep are probably eaten as carrion, an assumption supported by the finding of dipterous pupae in association with wool in some scats.

Indigenous mammals found most frequently in seats were the Western Grey Kangaroo (*Macropus fuliginosus*) and the Brush Tail Possum (*Trichosurus vulpecula*). Large carcasses such as those of kangaroos may provide predators with many meals and once the hide is eaten the carrion may not be readily detected in scats. This problem may account for the large number of seats with unidentifiable mammalian remains (mostly bone) in the WNP collection. Kangaroo carcasses were seen frequently in heathland in WNP and many scats collected there contained unidentifiable bone material. *Macropus rufogriseus*, which is known to occur in LDNP, was not detected in any scats.

Small indigenous rodents (*Pseudomys apodemoides* and *Notomys mitchelli*) and marsupials (*Sminthopsis crassicaudata*, *Antechinus flavipes* and *Ningaui* sp.), roughly comparable in size to house mice, were of infrequent occurrence in the scats and another two species (*Cercartetus concinnus* and *Sminthopsis murina*) known to occur in the Parks were not detected. The low frequency of occurrence of small indigenous mammals in the seats may reflect low densities of these animals in the Parks, or that these species may not be preferred prey items of foxes.

The level of predation on birds may be underestimated because scats were not collected in spring when the eggs and nestlings of ground nesting species would be vulnerable. The presence of shell fragments in some seats indicates that eggs are taken; and Frith (1962), in a study carried out in New South Wales, reported that predation by foxes on Mallec Fowl eggs (but not adult birds) was high. No explanation for the difference in levels of predation on birds in the two Parks is obvious.

At the time this study was carried out foxes were probably the major mammalian predators in both Parks. As in other areas where the diet of foxes has been studied, their preferred food items, in the absence of domestic stock, appear to be exotic mammals such as rabbits and house mice. While these species continue to be abundant in the Parks, the level of predation on native fauna will presumably remain relatively low and the need for control of predators unimportant. The

presence of foxes may be of value in controlling the numbers of rabbits and house mice in the Parks.

ACKNOWLEDGEMENTS

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TWO THALLOID (PROBABLY ALGAL) SPECIES FROM THE EARLY DEVONIAN OF CENTRAL VICTORIA

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ABSTRACT: *Buthotrephis trichotoma* sp. nov. is described from the Gedinnian or Siegenian lower part of the Humevale Formation at Kinglake West and *B. walhalla* sp. nov. from the Norton Gully Sandstone at Walhalla in sediments probably of late Pragian age. These species are interpreted as algal remains.

The algal flora, as well as the thalloid fossils of slightly uncertain biological affinity from the Devonian of Victoria were reviewed by Douglas (1981) and shown to be known from only a few described species; therefore, any new discoveries are worthy of reporting and it is the aim of this paper to expand knowledge of that flora.

Regularly branching impressions and compressions from Silurian and Devonian sediments of the Melbourne Trough in central Victoria have often been assigned to *Buthotrephis* (Chapman 1903, Lucas 1927, Opik 1953, Douglas & Paton 1972) (= *Bythotrephis* [sic] of several of these papers). However, in some cases these referenees are to specimens that are probably not fossil algae. For example, *B. tenuis* Hall 1852, from Silurian outcrop in the Botanic Gardens, Melbourne (Chapman 1903) (Fig. 1C), and *Bythotrephis* [sic] sp., from the Lower Silurian Wapentake Formation near Heathcote (Opik 1953, fig. 130), are most probably traces left by burrowing organisms as are specimens recently collected from the Dargile Formation near Heathcote (Fig. 1A, B). The distinction between fossils of this type and those of algal origin is very difficult but may be approached by attention to whether the fossil is a compression or is an infilled cavity.

We are grateful to Steve Eckart, and Frank and Enid Holmes for help with collecting the Kinglake species and Misses C. Donohue and P. Clark and Mr. C. Marshall for help with photography.

All the material is held in the Palaeontological Collection of the Museum of Victoria (prefix NMVP).

SYSTEMATIC PALAEOLOGY

Class THALLOPHYTA

Genus *Buthotrephis* Hall 1847

TYPE SPECIES: *Buthotrephis gracilis* Hall 1847.

REMARKS: *Buthotrephis* was discussed at length by White (1902) who was careful to point out that it was not his purpose "to strenuously urge that these fossils are marine algae, although I believe them to be such". The circumstantial evidence that he quoted was "a, the marine habitat, b, the typical algaloid form of development and growth and c, the aspect of the residue". The same applies to the Victorian forms described below.

Schweitzer (1983) provided a modern discussion of the genus; it is not the aim of this paper to review concepts of the several related algal genera but rather to acknowledge that these two species comply with the original diagnosis and point out a possible subdivision of the genus.

Buthotrephis trichotoma sp. nov.

Figs 2, 3

ETYMOLOGY: Named for 3-branched division of lobes near base.

MATERIAL, LOCALITY AND AGE: Holotype NMVP107493. Paratypes NMVP107494 to 107499. From recent excavation of an old quarry known previously as Davies or Middendorp's Quarry (see Jell 1983) on the western branch of Stony Creek about 1.6 km north of Kinglake West State School, and 100 m north of the creek crossing on Kestrel Lane, 40 km north-northeast of Melbourne. The specimens come from a single laminar-bedded sandstone that also yields large amounts of plant chaff and a few fragmentary animal fossils. This horizon is included within a siltstone unit several metres thick that is very rich in marine fossils (brachiopods, corals, trilobites, echinoderms, etc.). This unit is believed to have been deposited by a series of catastrophic events (Jell 1983). Thus these fossil plants are most probably marine and are regarded as having been ripped up and transported to the site of deposition.

The age of this horizon is Early Devonian, probably Gedinnian or Siegenian (Holloway & Jell 1983, Jell 1983).

DIAGNOSIS: Member of *Buthotrephis* with lobes dividing into three branches near base, followed by repeated dichotomous branching away from main stem.

DESCRIPTION: Whole thallus and base of attachment unknown. Fossils generally representing lobes up to 60 mm long and wide, all flattened and without bases. One specimen (Fig. 2) shows three branches arising from a main stem that appears to taper slightly downwards; it has up to 10 longitudinal ridges which, although probably the result of compression, indicate a thicker section than in rest of lobe, with branches dividing dichotomously 15 mm away from this main stem. Other lobes

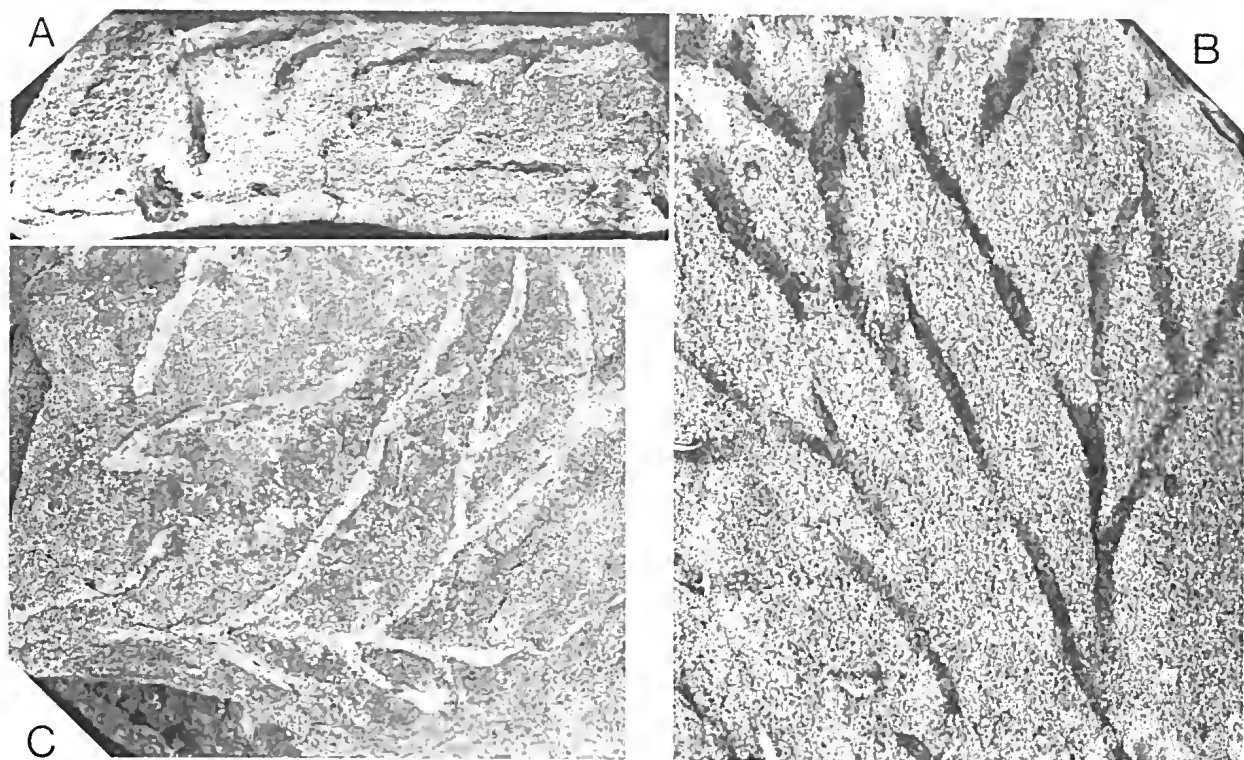


Fig. 1—Horizontal burrows forming structures that resemble *Buthotrephis*. A, B, lateral (bedding planes across page) and planar views respectively, of specimen from Dargile Formation showing darker burrows crossing bedding planes X 1. C, planar view of specimen described by Chapman (1903) as *Buthotrephis tenuis* Hall 1852, NMVP2979, X1.

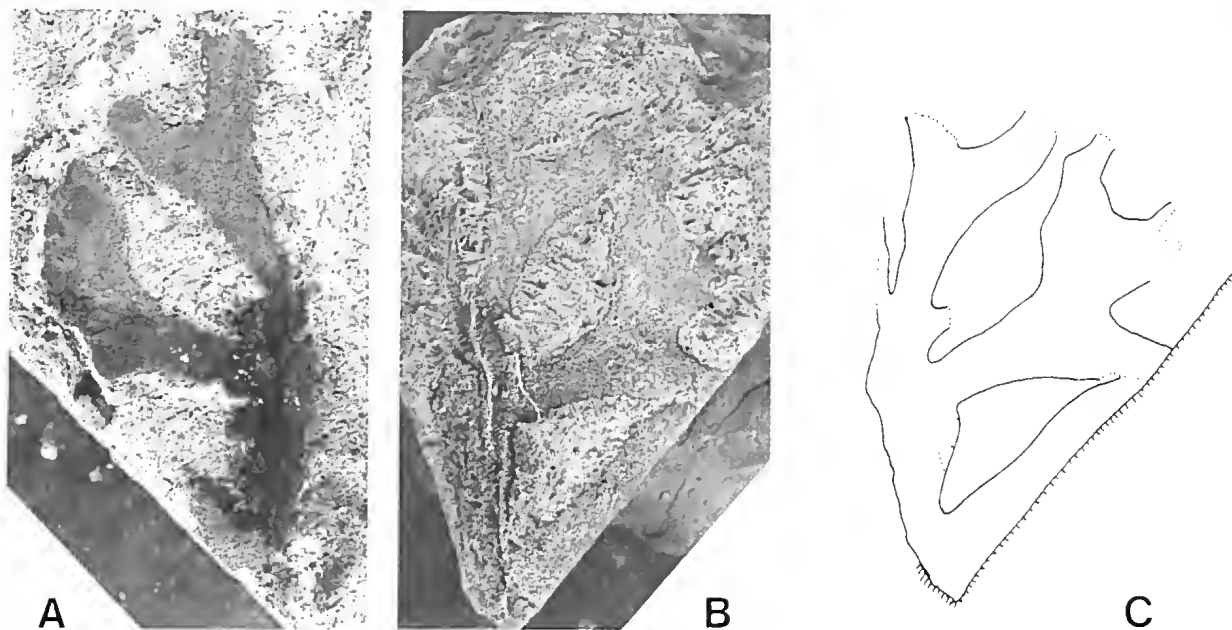


Fig. 2—*Buthotrephis trichotoma* sp. nov. NMVP107498, X1.8. A, different iron minerals produce the different colours on the fossil. B, counterpart, whitened with ammonium chloride to show the erumped longitudinal ridges in vertical stem. C, sketch of B to show branching pattern; broken edges of fossil denoted by dotted lines, feathered line is edge of specimen.

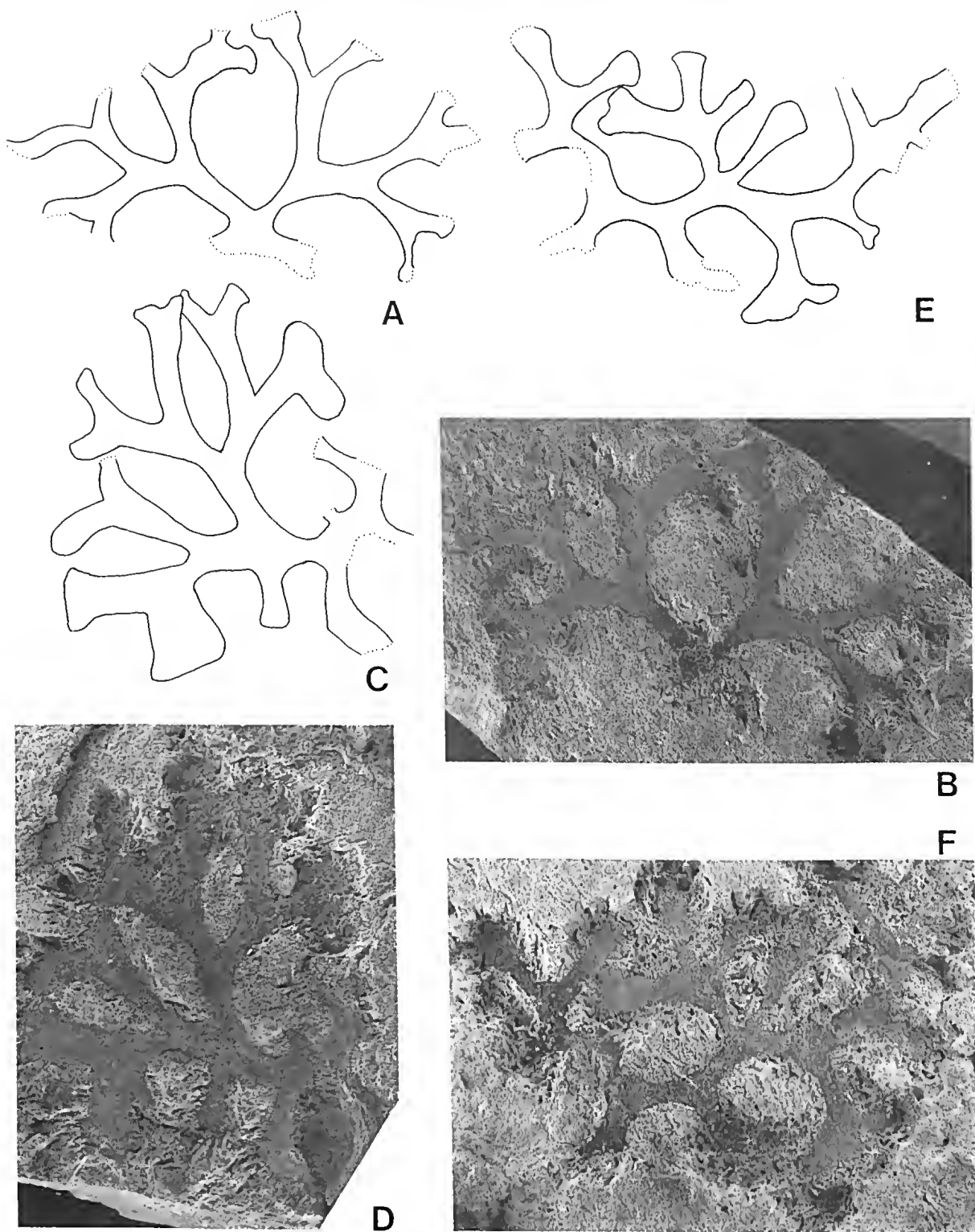


Fig. 3—*Buthotrephis trichotoma* sp. nov. A, B, NMVP107494, outline sketch and unwhitened view respectively; dotted lines indicated broken edges of specimen, X 1.2. C, D, NMVP107499, outline sketch and unwhitened view respectively X 1.2, E, F, NMVP107493, holotype, outline sketch and unwhitened view respectively, X 1.2

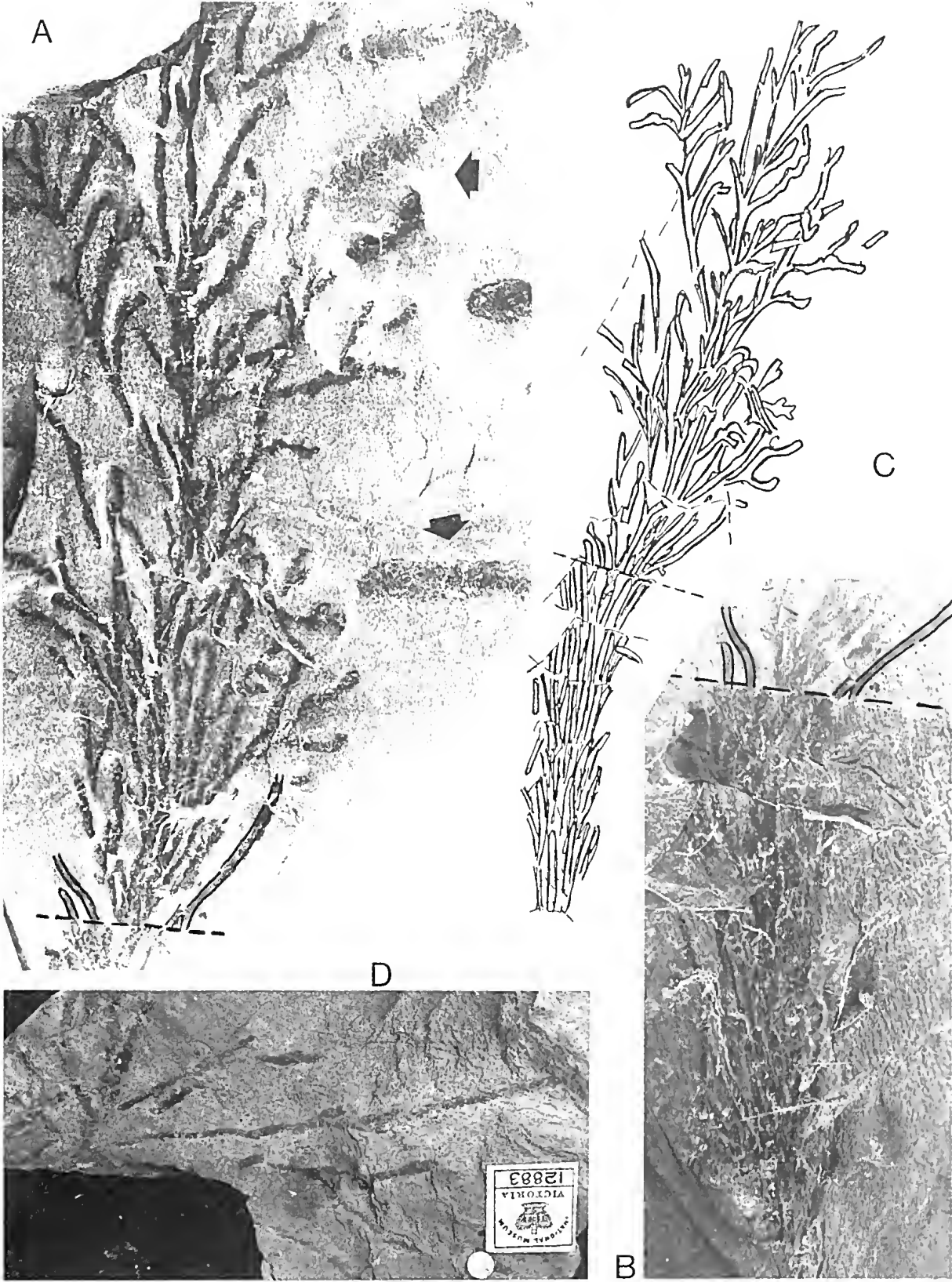


exhibit one or two strongly curving branches that may divide or give off single side branches which themselves divide. Near base of two largest lobes (Fig. 3D-F) are some trichotomous divisions but they are less common (2 in one individual; 1 in other). Distance between successive dichotomies ranging between 8 and 15 mm; width of stem away from dichotomies varying from 3 to 6 mm; tips of branches expanded laterally and lobate.

REMARKS: This species displays considerable variation in form of the lobes and in type of branching but there appears to be an obscure central stem in some specimens. Almost all species of *Buthotrephis* including the type, possess longer and, in most cases, narrower lobes and have greater distance between successive branching points. *Buthotrephis divaricata* White 1902 not Kidston 1886 from the Late Silurian of Indiana is the most similar species being comparable in overall size, in lobe width and, for the most part, in style of branching (e.g., the distal forking of almost every lobe). However, it may be distinguished by the thallus form of numerous lobes branching only once, rarely twice, above the base and the absence of any suggestion of a central stem. We concede that future discoveries emphasizing a considerable range of variation may lead to synonymy of the two species. In that case it should be noted that *B. divaricata* was preoccupied (Kidston 1886) and *B. trichotoma* should include White's specimen (1902, p. 16).

Distinction of *Hungerfordia* Fry & Banks 1955 from some species of *Buthotrephis* may depend on knowledge of the basal parts and differentiation between *B. trichotoma* and *H. dichotoma* Fry & Banks 1955 is an example. *Buthotrephis trichotoma* and *B. divaricata* White with wide, relatively short lobes, each with few dichotomies, may prove to be generically distinct from *Buthotrephis* and may possibly be better accommodated within *Hungerfordia*; this may be assessed when the bases of these two species become available.

Yeaia flexuosa Douglas 1983 from the Upper Silurian of the Melbourne Trough is a dichotomously-branching alga but the long intervals of up to 100 mm between dichotomies giving the branches a long strap-like form distinguish it from *B. trichotoma*.

Buthotrephis walhalla sp. nov.

Fig. 4

1912 *Bythotrephis* [sic] *divaricata* Kidston; Chapman, p. 231, pl. 38, fig. 1.

1981 Large thallus. Douglas, p. 10, pl. 3, fig. 10.

ETYMOLOGY: A noun in apposition.

MATERIAL, LOCALITY AND AGE: Holotype NMVP52501. Paratypes NMVP48927, 175698, 175699. All are from 200 m below the surface in New Long Tunnel Adit, Walhalla at GR433213 on Walhalla (851D) 1:31680 topographical map; they occur as thin black

impressions on a sheared and disrupted grey-black siltstone bed of the Norton Gully Sandstone, Walhalla Group. The age of this horizon, based on stratigraphic relationship to graptolite faunas, is tentatively put at Late Pragian (i.e. Early Devonian).

DESCRIPTION: Thallus compressed, upper part branching sub-dichotomously, branches long, narrow and flexuous, width 1-2 mm, margins undulate, sometimes contorted to form small protrusions. Thallus length 200 mm or more, elongated, fan-shaped; basal stipe with straighter unbranched segments of 10-20 mm length, arising at acute angle and forming thick dense mass.

REMARKS: The holotype provides new information on the base of the thallus which may or may not be pertinent to other members of the genus, which, with very few exceptions, is known only from distal fragments of the thallus. The close pressed linear segments around the base give this part of the new species a very different appearance to the rest of the fan-shaped thallus. It is superficially similar to the stem of the lycophyte *Baragwanathia longifolia* Lang & Cookson 1935. On the same specimen (Fig. 4A) are remnants of a larger fossil (arrowed) that appears to branch similarly to *B. walhalla* and could well belong to one of the larger species of *Buthotrephis* with wider lobes such as *B. flexuosa* Hall 1847.

Among species of *Buthotrephis* none could be confused with *B. walhalla* in features of the basal part; but in more distal parts of the thallus forms such as *B. subnodosa* Hall 1847 and *B. rebskei* Schweitzer 1982 are quite similar to *B. walhalla* in numbers of forks and in thickness of lobes. However, the average distance between forks is less in *B. walhalla* than in those other species. The closest form is probably *B. subnodosa* whose subnodulose form of the lobes is shared by the new Victorian species.

Maceration to find anatomical features for classification provided no cuticular remains and this in itself provides meagre negative evidence for the assignment of these fossils to the Thallophyta.

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Fig. 4—*Buthotrephis walhalla* sp. nov. A, B, upper and lower parts respectively, of holotype thallus (dashed line common to the two prints), NMVP52501, X1 and X1.1 respectively. Arrows on A point to fragments of a much larger specimen of *Buthotrephis* possibly *B. flexuosa* Hall 1847. C, line drawing of holotype, NMVP52501, X 0.7. D, fragmentary specimen described by Chapman (1912) as *B. divaricata* Kidston from Vale's Adit, Walhalla, NMVP12883, X 1.1.

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MYODELTHYRIUM, A NEW PERMIAN GENUS OF THE SYRINGOTHYRIDACEA FREDERIKS 1926 (BRACHIOPODA)

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ABSTRACT: *Myodelthyrium* is proposed as a new generic name for a syringothyridacean species originally placed in *Pseudosyringothyris* Frederiks 1916. The type species is *M. dickinsi* (Thomas 1971). Its distinguishing structures include a pair of muscle scars on the inside of the delthyrial plate.

The distinctive West Australian Permian species *Pseudosyringothyris dickinsi* was described by Thomas (1971). The species was earlier reported in an unpublished Ph.D. thesis of the University of Melbourne by Thomas in 1961. This species is a prominent constituent of the Early Permian (Sterlitamakian) faunas of the Callytharra Formation of the Carnarvon Basin. It is also known from the Canning Basin and is a useful index fossil for interbasinal correlation.

The species is clearly a member of the spiriferid superfamily Syringothyridacea Frederiks 1926, as interpreted by Ivanova (1972), characterised by punctate (mostly) spiriferids with high ventral interareas, simple lateral costae, generally smooth ventral sinuses and smooth or medially-grooved fastigia. *Syringothyris* Winchell 1863 and *Pseudosyrinx* Weller 1914 are representative of the 20 or so genera now included in the superfamily. Many are large forms.

Thomas (1971) ascribed *P. dickinsi* to *Pseudosyringothyris* Frederiks 1916, provisionally accepting the interpretation of Gobbett (1964, p. 174) that his punctate species *P. borealis* Gobbett as well as an unnamed species from the Permian (Svalbardian) Spirifer Limestone of Spitzbergen belonged in *Pseudosyringothyris*. The Spitzbergen species possess a median longitudinal ridge on the inside of the delthyrial plate, with depressions on each side.

Frederiks (1916) erected *Pseudosyringothyris* as a subgenus of *Cyrtia*, type species *Cyrtia (Pseudosyringothyris) karpinskii* Frederiks 1916. His English summary reads: "Shell large, transverse; hinge line straight, usually as long as the greatest breadth of the shell; area high flat; sinus deep and wide; surface ornamented by many radial ribs. Internally between the dental plates in the delthyrium is a transverse delthyrial plate, which has on the interior side a roller-like callosity, called a pseudosyrinx" (sic). The pseudosyrinx was considered by Frederiks (1916, p. 49) to represent a stage in the evolution of the syrx. The roller-like callosity was illustrated in a section (Frederiks 1916, fig. 16 and plate 3, fig. 9a), reproduced in Thomas (1971, fig. 47). This structure is a shell thickening of the inner delthyrial plate with a median depression. Thomas (1971, p. 127, p. 138) regarded it as an adventitious secondary thickening similar to that shown in some specimens of *P. dickinsi* (Thomas 1971, fig. 55g). How-

ever, one of Frederiks' illustrations (Frederiks 1916, pl. 3, fig. 1d) seems to show a longitudinal median ridge on the inner delthyrial plate.

Pseudosyringothyris karpinskii was based on a small collection (1-2 specimens apparently) distinguished from the more numerous examples of *Cyrtia kulikiana* Frederiks 1916. All were collected from the Bolshezemelskaya Tundra of the northern Urals, U.S.S.R. The types of *P. karpinskii* and some of the specimens of *C. kulikiana* came from the Adzva River area. Frederiks noted the close resemblance of the two species but distinguished *P. karpinskii* on its pseudosyrinx, the outline of the umbo and the finer, sometimes dichotomous, ribs.

Pseudosyringothyris has been recognised in the Permian of the USSR by some Russian authors. Ivanova (1960) listed it with a brief diagnosis but without illustration as comprising only the type species, from the Bolshezemelskaya Tundra and from Novaya Zemlya. Solomina (1970) described a new species *P. inopinatus* from Northern Verkhoyan without illustrating or describing the internal delthyrial features. Zavodovskii (1970) described three species from north-eastern USSR: *P. inopinatus* and two new species *P.(?) russiensis* and *P. parenensis*. The inner delthyrial structures were not described or illustrated. Kalashnikov in Kalashnikov and Ustritskii (1981) provisionally included a new species *P.(?) ustritskyi* which appears to lack a delthyrial plate.

Grigoryeva (1977), in a comprehensive review of the liharewids of Siberia and the Arctic, was critical of the use of *Pseudosyringothyris* by Gobbett (1964) and by Thomas (1971). She stated that the validity of *Pseudosyringothyris* is uncertain because *P. karpinskii* is said to be indistinguishable from *C. kulikiana* (Frederiks), the type species of *Cyrtella* Frederiks 1924. Extensive collecting by Ivanova (1972) from the topotype areas of both species has failed to provide any more examples of Frederiks' "pseudosyrinx" structures. *Cyrtella kulikiana* Frederiks is reported by Grigoryeva (1977) and by Grigoryeva and Kotlyar (1966) to possess a false or pseudodelthyrial plate, formed by internal secondary thickening in the delthyrial region.

From my enquiries in Leningrad in 1968, Frederiks' type specimens appear to be no longer available. In consequence, because of the uncertainties of the validity

of *Pseudosyringothyris* and of its internal delthyrial features, a new genus *Myodelthyrium* is proposed, type species *P. dickinsi* Thomas. Its principal distinguishing feature is the presence of a pair of strong oval muscle scars on the inside of the delthyrial plate, separated by a median longitudinal ridge.

SYSTEMATIC PALAEOONTOLOGY

Order SPIRIFERIDA Waagen 1883

Suborder SPIRIFERIDINA Waagen 1883

Superfamily SYRINGOTHYRIDACEA Frederiks 1926
(sensu Ivanova 1972)

Family LICHAREWIIDAE Slyusareva 1958
(sensu Grigoryeva 1977)

Genus *Myodelthyrium* gen. nov.

TYPE SPECIES: *Pseudosyringothyris dickinsi* Thomas 1971.

ETYMOLOGY: mys, myos, a muscle; delos, visible; delthyrium, a door. Greek, masculine.

DIAGNOSIS: Large finely punctate syringothyridaceans resembling *Pseudosyrinx* Weller externally, high ventral interarea with perideltidium, smooth sinus and fastigium; numerous simple lateral costae. Internally with considerable apical callosity, short divergent adminicula and longer dental flanges both with thin initial components; well developed delthyrial plate with a pair of elongate oval muscle scars on the inside, separated by a median longitudinal ridge; dorsal cardinalia massive with recurved socket plates and strong crural plates; micro-ornament of fine short radial striae interspersed with oval to pear-shaped pustules.

SPECIMENS OF THE TYPE SPECIES: The holotype CPC 1636 and other illustrated specimens CPC 1634, 1635, 1637-1644 are in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Geology and Geophysics, Canberra, A.C.T.

REMARKS: The diagnosis and description of the type species include the above features and are sufficiently

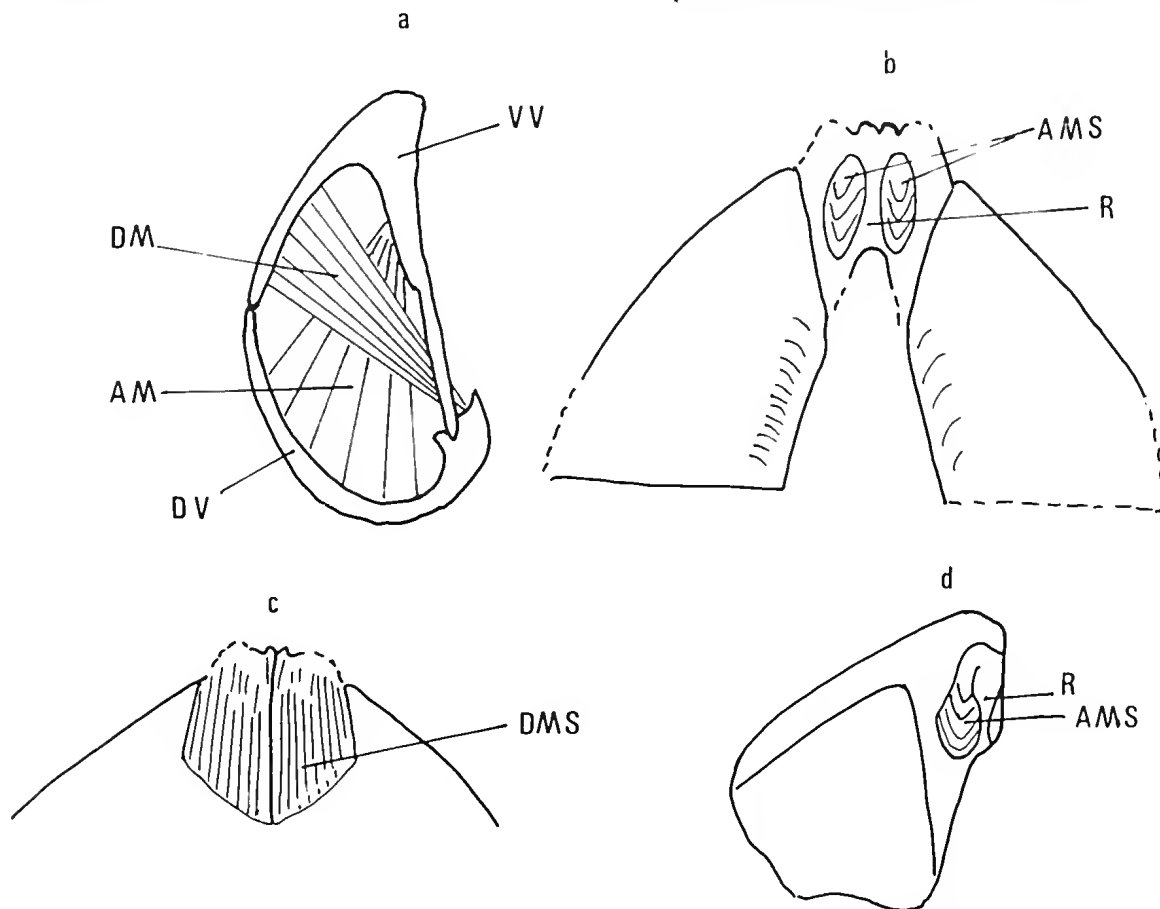


Fig. 1—*Myodelthyrium dickinsi* (Thomas) (modified from Thomas 1971, fig. 54). (a) Semidiagrammatic sketch of shell ($\times 0.75$), longitudinal profile section showing inferred muscle system; VV ventral valve, DV dorsal valve, AM adductor muscles, DM diductor muscles. (b) dorsal view of internal mould CPC 1639 ($\times 1$), showing adductor muscle scars AMS and median ridge R on inside of delthyrial plate. (c) ventral view of same mould ($\times 0.9$) showing diductor muscle scars DMS. (d) dorsal (internal) view of incomplete ventral valve CPC 1644 ($\times 0.9$) showing adductor muscle scar AMS and median ridge R. Specimens CPC 1639 and CPC 1644 are also illustrated in Thomas (1971, pl. 12, fig. 3a, b and pl. 10, fig. 5 respectively).

covered in Thomas (1971, p. 140-148). Later, more extensive, collections have been made from the Callytharra Formation by the author. They confirm the presence of a large species with high flat to gently incurved interareas up to 6.5 cm high and over 11 cm wide. On the inside of the large delthyrial plate is a pair of oval striated muscle scars separated by a median longitudinal ridge (Fig. 1b, d). The delthyrial plate has a thin outer transverse initial component supported internally by shell thickening (Thomas, 1971, p. 146 and figs. 55, 56). It can be regarded as a "true" delthyrial plate in contrast to the "false" or pseudodelthyrial plate described by Grigoryeva and Kotlyar (1966) and Grigoryeva (1977) formed by apical shell thickening only. A stegidium is present in front of the delthyrial plate in one specimen, the holotype, Thomas (1971, p. 11, fig. 1c).

Thomas (1971, p. 146 and text fig. 54) presented arguments that the muscle scars on the delthyrial plate are the site of attachment of the ventral adductor muscles. Fig. 1a shows a reconstruction of the muscle system after Thomas (1971, text fig. 54). The ventral valve internal mould in Fig. 1b, c shows little indication of adductor muscle scars in the median position except possibly in the posterior part between the longitudinally-striated diductor muscles. Other specimens show that the adductor muscle scars can be situated more posteriorly on the delthyrial plate and hence closer to the diductor scars. The position would be dependent on the slope of the interarea.

Comparable oval depressions separated by a median ridge are present on the inside of the delthyrial plate in *P. borealis* Gobbett (1964, plate 24, fig. 3). I have examined some of Gobbett's specimens (but not the holotype) in the Riksmuseum, Stockholm and confirm the presence of these depressions but striations were not noted. *Pseudosyringothyris borealis* therefore possibly belongs in *Myodelthyrium*. Further comparison with Gobbett's type specimens is desirable for confirmation.

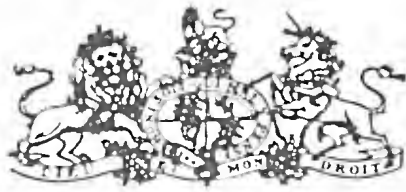
Similar delthyrial structures have not otherwise been recorded but it is possible that they are present in other syringothyridacean species with high interareas suitably inclined to the dorsal valve. The internal delthyrial features of many species have not been recorded.

ACKNOWLEDGEMENTS

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LAVA FLOWS OF MOUNT ROUSE, WESTERN VICTORIA

By C.D. OLLIER

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ABSTRACT: Mount Rouse, an extinct volcano located immediately south of Penshurst in Western Victoria, was a source for copious lava flows which followed several pre-existing valleys and reached the coast 60 km to the south. Many typical features of drainage modification are associated with the lava flows. Stony rises are widespread and interpreted to mean that a lava tube mechanism was in operation when the lava was flowing, and indeed was necessary to produce such long flows. If this is so, eruption of all lava occurred in a very short time. A new date for the volcano is 1.8 m.y., which is inconsistent with ages of about 0.3 m.y. reported from basalts near Port Fairy. The Mt Rouse flows serve as a useful marker in distinguishing Pleistocene from older volcanoes in the region. The Mount Rouse basalt has suffered very limited weathering: the basalt of the nearby Mount Hamilton land-system, which is about twice as old, is very much more weathered.

The Western Plains of Victoria contain many volcanoes, and are largely covered by a veneer of basalt. There are about 200 points of eruption on the plains, and they range in age from several million years old to about 15 000 years for Tower Hill (P. Kershaw, pers. comm.). The area is a distinct volcanic province characterised by areal or polyorific volcanicity. The volcanoes are numerous but small, and each was active only once, and then for a short time. This contrasts with the central volcanic type of eruption, in which eruption may continue at the same site for millions of years. The general sequence of eruption at volcanic centres of the Western Plains of Victoria was first a highly explosive eruption to produce a maar, then effusion of very fluid lava which flowed down valleys and spread over plains if sufficiently voluminous, and finally the build-up of a scoria cone. Some points of eruption do not show all three phases, and occasionally other landforms (such as lava cones) may be built.

Some of the volcanoes and flows have been dated by radiometric methods. Relative dates for some have been deduced by examining the degree of weathering and erosion, and the relative disruption of drainage patterns. In the far west, for instance, Mt Clay and Mt Vandyk are very old and deeply weathered with very few rock outcrops. Mt Eeles, on the other hand, only about 20 000 years old (Ollier 1981), has hardly any weathering and its original flow structures are preserved almost intact. In between come many volcanoes and flows with intermediate degrees of weathering and erosion. Gibbons and Gill (1964) postulated a relative sequence of groups of volcanoes based on the nature of the volcanic landscape, essentially the depth of soil and the preservation of stony rises. The same technique is described further by Gibbons and Downes (1964).

This paper is about the lava flows of Mount Rouse, which have intermediate weathering and erosion, and are part of the Giringurrup land-system of Gibbons and Gill. Mt Rouse is located just south of Penshurst and about 10 km east of Hamilton (Hamilton 1: 100 000 map, grid reference 142062). The scoria cone is about

100 m above the surroundings, and has an elevation of 370 m above sea level. Mount Rouse is a composite volcano, mainly built of scoria but with a few interbedded flows. To the south of the scoria cone lies a lower, well-defined, basalt-rimmed crater [Fig. 4, also figured in Ollier & Joyee (1964)]. Lava from Mount Rouse occurs in two large patches, connected by narrow lava-filled channels. One large patch lies immediately south of the volcanic cone; the other is farther to the south and reaches the coast (Fig. 1).

LAVA FLOWS

Only a small amount of lava flowed north of Mount Rouse, but one patch extended about 4 km to the northwest and filled a valley head. A small lateral stream called Penshurst Creek on Fig. 2 flows along the northern edge of the lava lobe, away from the volcano and into Buckley Swamp. Buckley Swamp was created when the younger Mount Napier volcano blocked the drainage of this area. Before that, Penshurst Creek was probably a tributary to a river that flowed under the site of Mount Napier to the Harman Valley, but it may alternatively have been an upstream continuation of Muddy Creek.

Along the Eumerella River, which marks the northwest edge of the Mount Rouse lava flows, the lava appears to have simply banked up against old topography, for the pre-basaltic drainage was largely to the south and there were no convenient valleys to follow to the west.

Due southeast of the eruption point, a lava flow followed the valley of Spring Creek, and south of this, two other narrow strips of lava followed Whitehead Creek, and Whitehead South Creek.

The northern mass of lava drained south through two main valleys, now occupied mainly by Back Creek and the Moyne River. The Back Creek lava flow route is the simplest. The flow becomes more and more confined until, at its narrowest, it is only 200 m wide. The flow is less than 1 km wide over a distance of more than 5 km and then spreads out, originally overtopping low

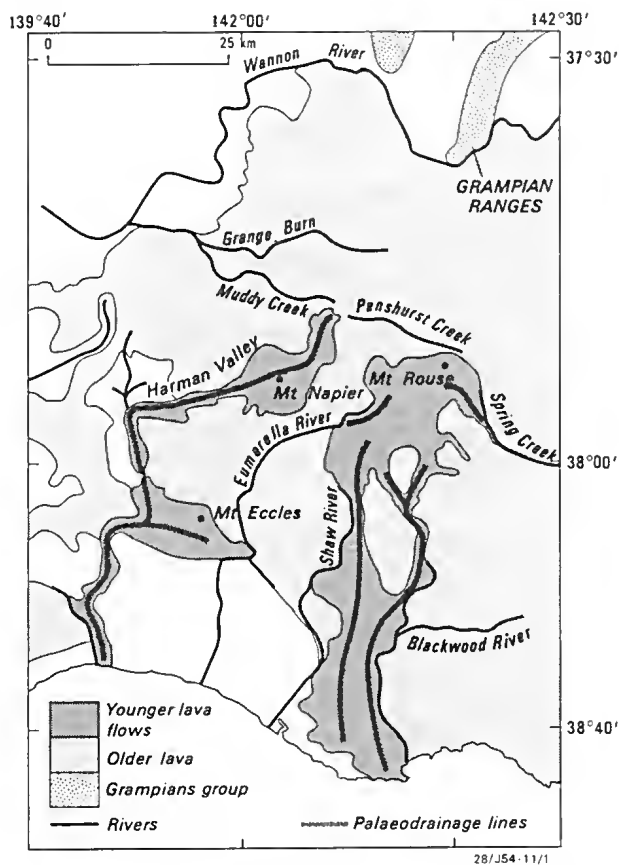


Fig. 1—The geomorphic setting of the Mount Rouse lava flow.

divides, and follows several different creeks. Some inter-fluvial areas are now "islands" of bedrock surrounded by lava flows (steptoes).

The Moyne River lava flow route is more complex, with two lava flows, labelled the Wandilla and the Glenlevitt, surrounding the Moorilah Steptoe (Fig. 5) and then uniting as the Moyne River lava flow. Over a distance of 6 km this flow is less than 1 km wide, but then it widens out and joins the Back Creek flow. The Coomealla Steptoe, 19 km long, was formed between the two flows. The united lava flow then continues south, getting wider, until at the coast its width is about 14 km.

DRAINAGE MODIFICATIONS

The Rouse flow provides splendid examples of drainage modifications such as diversion, lateral streams and twin lateral streams. The Eumerella is a fine example of a lateral stream, following the edge of the lava for about 15 km, not including the small meanders. The stream then leaves the lava edge, possibly following its pre-lava course. Twin lateral streams can be found at all scales (Fig. 2). At a large scale, the Shaw River and the Moyne River are lateral streams on the main Rouse flow where it enters the sea, though each is in fact more complex in

detail. On a medium scale, Back Creek and Shaw River North are good examples, and on a small scale Whitehead Creek is excellent, with two streams flowing parallel for 7 km on opposite sides of a lava flow less than 200 m wide.

Successive diversion is shown by the sequence starting with the Shaw River North, which, after being a lateral stream, is diverted into the Carmichael, which in turn is diverted into the Kangaroo Creek, and finally becomes the Shaw River Central (Fig. 2).

A few rivers manage to cross lava flows from one side to the other: the Moyne River does it several times.

The inliers (steptoes) are also commonly bounded by streams, such as the Back Creek and the Moyne River bounding the Coomealla Steptoe, and the twin streams bounding the Moorilah Steptoe (Fig. 5). Even quite tiny steptoes are often bounded by streams on at least one side.

PALAEODRAINAGE

Evidently the flows from Mount Rouse were poured over an initially flat topography with narrow, little-incised streams, and a generally southern slope so that most lava flowed in that direction. By interpolating streams between twin laterals; locating old streams where the lava has a lobate outline; and, by making reasonable guesses where lava has overtopped divides, it is possible to make a reasonable reconstruction of the pre-basaltic drainage pattern. This pattern is shown in Fig. 3 and is essentially a simple dendritic pattern showing southward drainage from a divide in the vicinity of the present Mount Rouse.

Even this old drainage was on a landscape modified by earlier lava flows. A large lava flow of unknown source had disrupted earlier drainage from the north, and the River Wannon is a lateral stream with an east-west course along the northern edge of this lava plain. The younger Mount Napier eruption blocked drainage going southwest, forming Buckleys swamp, but not apparently diverting any water into the catchment of the streams associated with the Mount Rouse lava flows, for there is a low watershed between the Buckleys Swamp-Weerangourt drainage and the Eumerella drainage (Fig. 2). Nevertheless it seems that the Mount Rouse eruption occurred on relatively high country between the drainage going to the Wannon, to the proto-Eumerella, to Spring Creek, and south to the proto-Shaw and proto-Moyne (Fig. 1). It is not yet clear why the Blackwood River has an east-west course in this region of generally north-south drainage, but in any case, the lava did not follow it.

SURFACE FEATURES OF THE LAVA PLAIN

Almost everywhere the surfaces of the Mount Rouse flows are distinguished by stony rises, a term given to rough, rolling topography with mounds or ridges and intervening depressions. The difference in height between the hollows and the rises is usually about 3 m but can be up to 10 m, and the distance between adjacent rises is usually 15-30 m but may be over 100 m.

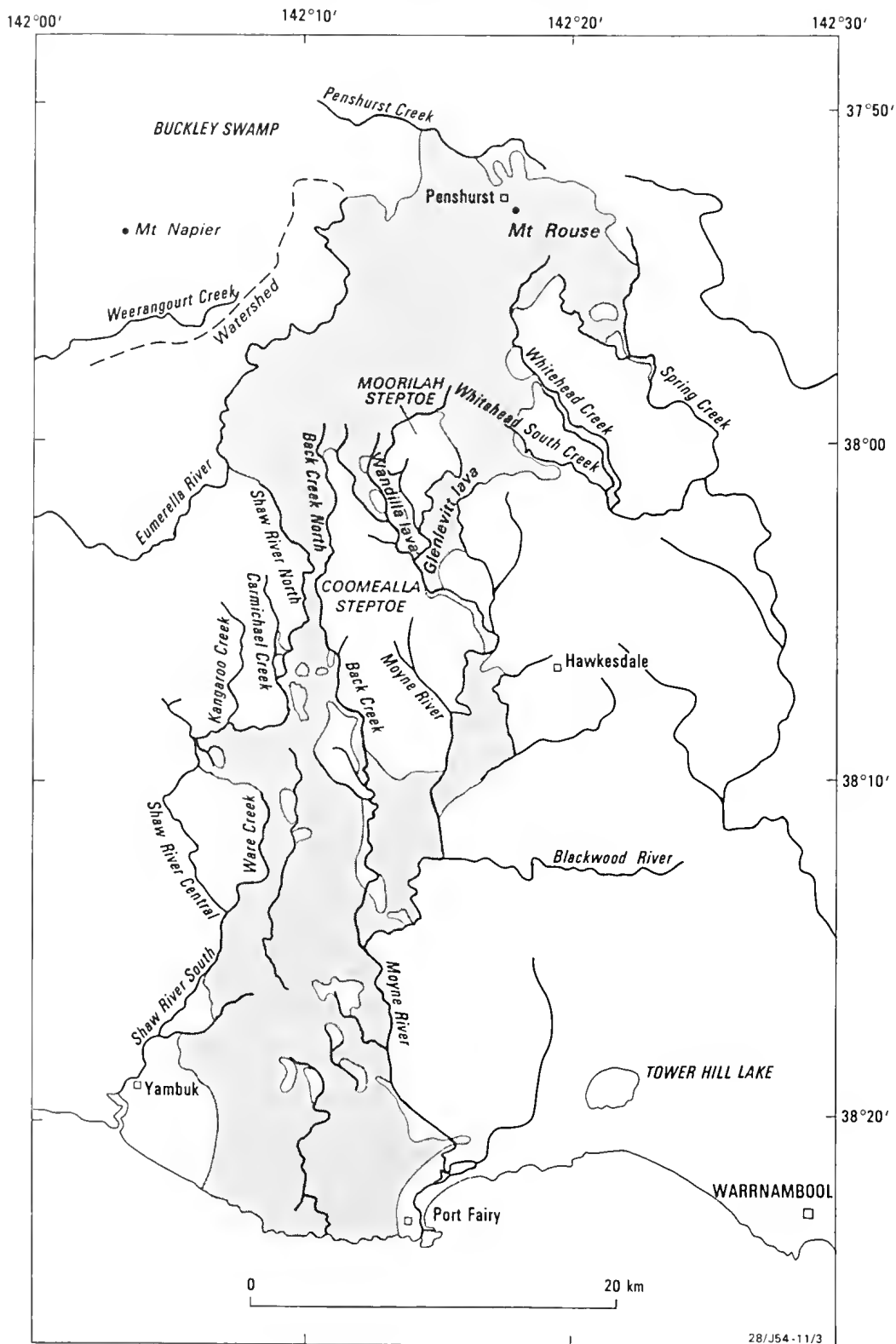


Fig. 2—The Mount Rouse lava flows and associated drainage.

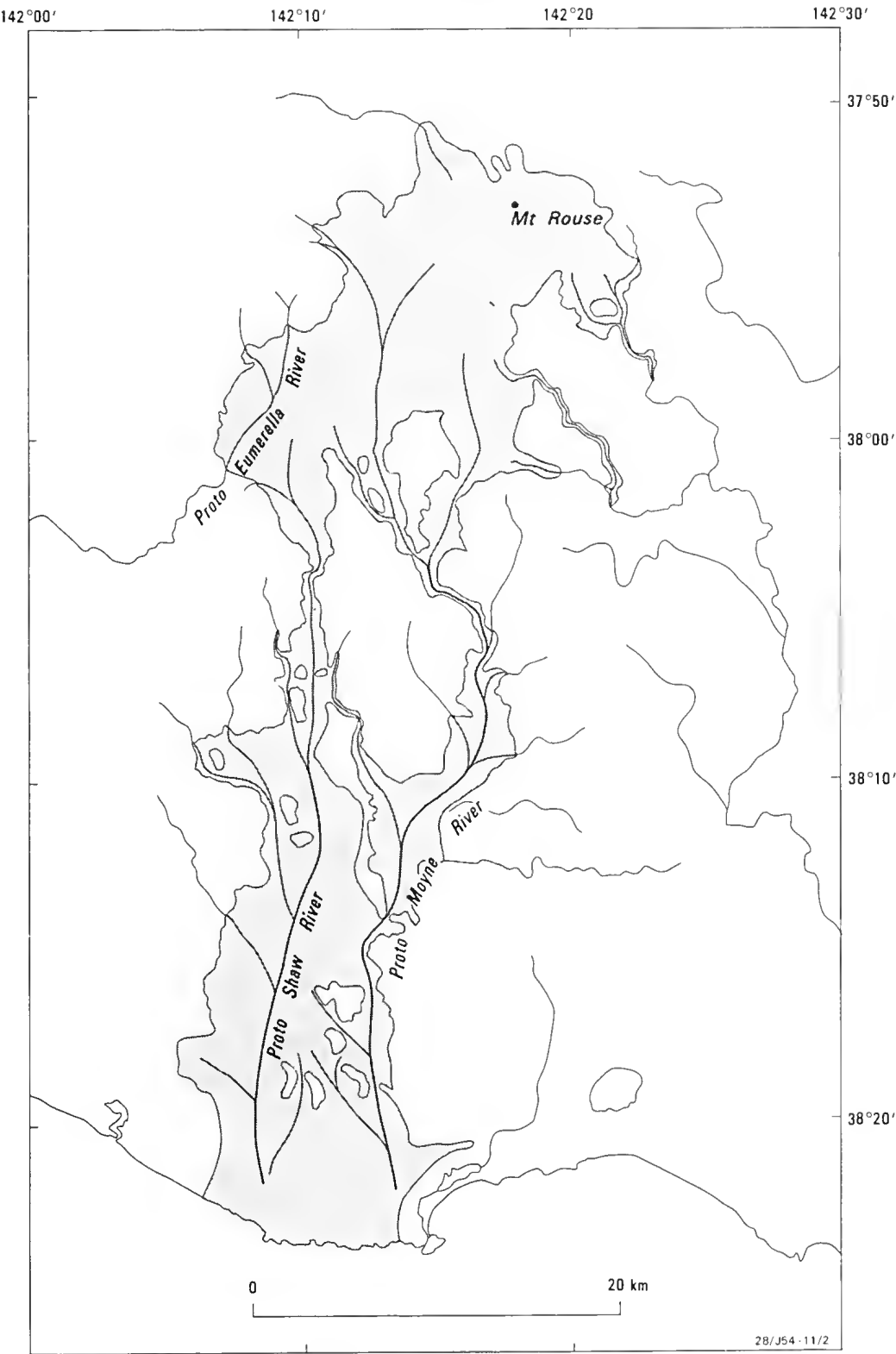


Fig. 3—The drainage of the area between Penshurst and the coast as it was immediately before the eruption of Mount Rouse.

The surface often consists of short columns, and the jointing suggests that the surface was once flat, with joints perpendicular to it, and that the carapace was draped over the rises as lava was withdrawn beneath the depressions. The pattern of mounds and depressions suggests that hot liquid lava flowed in a braided network beneath a crust of cold, fairly rigid lava, which was still sufficiently plastic to bend when lava was eventually withdrawn from the tubes.

WEATHERING AND SOIL

Gibbons and Downes (1964) describe the topography and soils of the Mount Rouse flow as part of the Girringurup Land-system. On the rises are reddish ochreolate soils, with abundant boulders and "floaters" of basalt. On the sides of the rises the soil becomes darker, and in the swales are black cracking clays, sometimes with carbonate. Gley soils are present in the wetter depressions. The soils have a relatively high base exchange capacity.

The country bounding the Rouse flow consists of what Gibbons and Downes mapped as the Greenhills Land-unit of the Hamilton Land-system, which is formed on basalt. The Land-system has flat topography, with no trace of stony rises although it is undulating in parts. It is weathered to a depth of up to 10 m and sometimes bauxitised. The weathered profile has an upper, strongly reddened and friable zone, an intermediate mottled zone, and a lower pallid zone above the altered rock. No ferrierite or other indurated zones are present. On the kaolinitic zone soils are either krasnozems or red solodic soils. Middle and lower slopes have brown solodic soils, and on the lowest sites are limited areas of prairie soils or chernozems.

THE AGE OF THE LAVA FLOWS

The age of the Mount Rouse flow has been estimated from the degree of erosion, weathering and soil formation. Although the basalt is weathered to the stage of spheroidal weathering, the soils still have a high content of exchangeable cations compared with those of the older flows in the area, which have been weathered to the kaolinitic stage. The stony rises are well preserved and the drainage little incised. In brief, the physiographic evidence suggests a young age. Gibbons and Gill (1964) thought that the flow might be within the range suitable for radio-carbon dating, which seemed a reasonable idea at the time, and suggested a Holocene age.

Jackson *et al.* (1972) suggested that the Girringurup Land-system (which includes the Mount Rouse flow) is less than 100 000 years old, the Dunkeld Land-system about 500 000 years, the Cobbobbonnee about 1 000 000 and the Hamilton about 4 000 000. The rocks of the Mount Rouse flow are generally unsuitable for dating by the potassium-argon method, because they are both vesicular and weathered. However, McDougall and Gill (1975) dated the Woodbine flow near Port Fairy, which seems to be part of the Rouse flow, and basalt from west of the Moyne River about 10 km north of Port Fairy. They reported the following ages:

PF 1 (Cape Reamur) 0.312 ± 0.005 m.y. (0.320 m.y.)

PF 2 (Port Fairy) 0.301 ± 0.008 m.y. (0.309 m.y.)

PF 10 (N of Port Fairy) 0.404 ± 0.017 m.y. (0.415 m.y.)
 0.438 ± 0.007 m.y. (0.450 m.y.)

(The figures in parentheses are ages calculated from new decay constants.)

The internal consistency of these dates suggests reliability. McDougall and Gill maintain that it is unlikely that the ages are too old, but do not discuss the possibility of them being too young. The inference that they have flows of at least two different ages is not consistent with the suggestion in the present paper that all the lava between Mount Rouse and the coast belongs to one flow.

The pyroclastics of the scoria cone at Mount Rouse are unsuitable for isotopic dating, but a single, fresh looking lava flow was found interbedded with the scoria, and was sampled for dating. This rock is a fine grained, slightly vesicular basalt containing 5-7% of small (generally <0.3mm) fresh olivine phenocrysts set in a fine-grained groundmass which exhibits a strong fluidal alignment of plagioclase laths. The laths, up to 0.2 mm in length and generally less than 0.02 mm wide, comprise about 30% of the groundmass. They are very fresh and probably of andesine composition. The remainder of the groundmass is very fine grained and contains abundant iron oxide granules (about 0.005 mm), fine pyroxenes and small clear patches of feldspar. The groundmass is holocrystalline and although not perfectly transparent (because of the fine grain size) it appears to be fresh and unaltered. The rock seems therefore to be suitable for total rock potassium-argon dating. It is unfortunate that no other sample has been found yet to provide another date for confirmation, so

TABLE I
K-AR ANALYSES OF LAVA FLOW FROM SCORIA CONE AT MT ROUSE

Sample	% K	$^{40}\text{Ar}^* (\times 10^{-11} \text{ moles/g})$	$^{40}\text{Ar}^*/^{40}\text{Ar}_{\text{total}}$	Age ($\times 10^6$ y)
Rouse-1	1.622	0.51293	0.426	1.82 \pm 0.04
Total Rock	1.620			

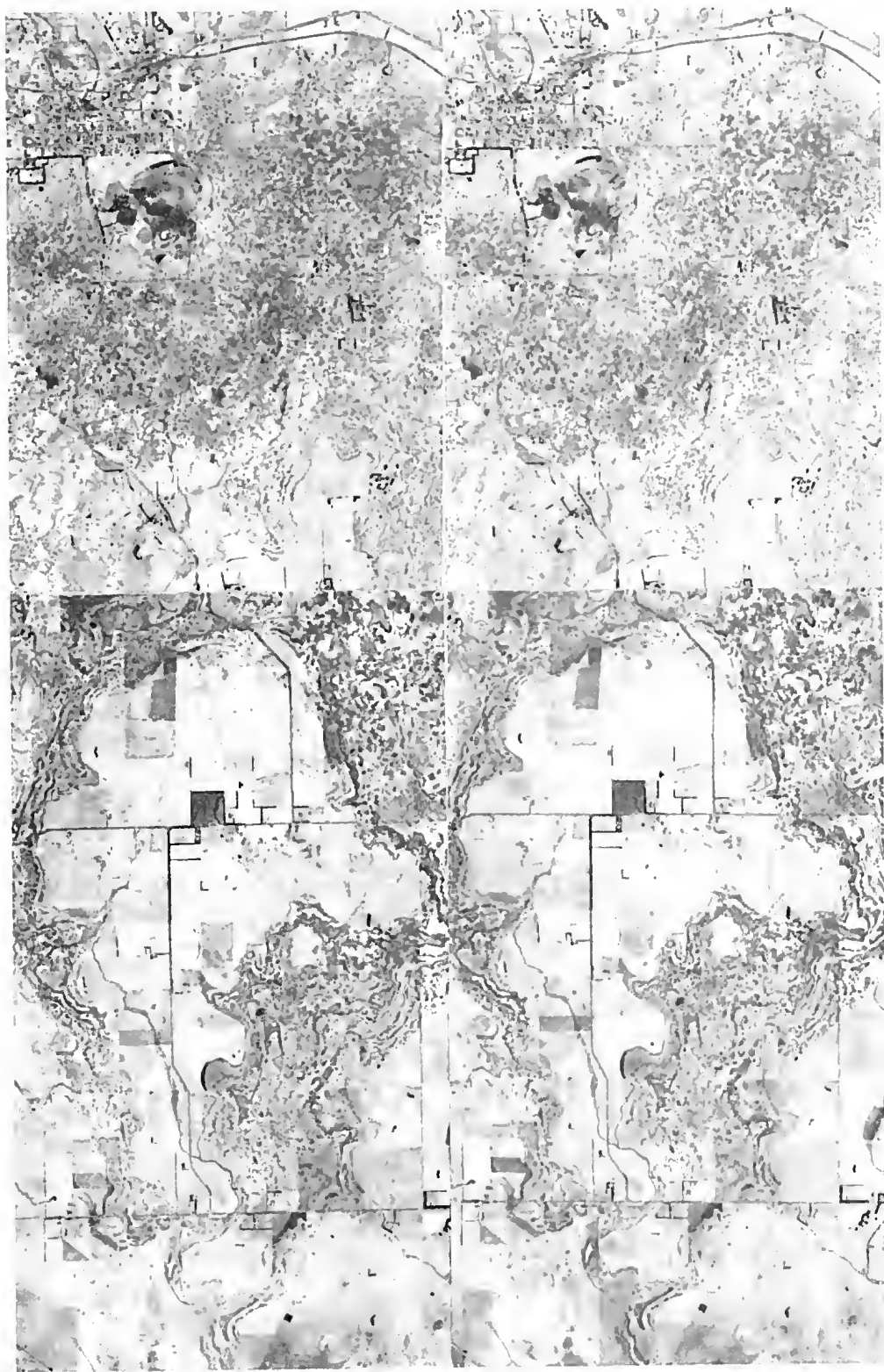
*Denotes radiogenic ^{40}Ar .

Errors are 1 standard deviation based on analytical uncertainties.

Constants used: $^{40}\text{K}/\text{K} = 1.167 \times 10^{-4} \text{ mol./mol.}$

$\lambda_{\beta} = 4.962 \times 10^{-10} \text{ y}^{-1}$

$\lambda_{\epsilon} = 0.581 \times 10^{-10} \text{ y}^{-1}$



for the present we must accept the single date. The result, provided by AMDEL laboratories, is 1.82 ± 0.04 million years. Analytical details are shown in Table 1.

The Plio-Pleistocene boundary was for a long time thought to be at 1.8 million years (e.g. Hays & Berggren 1971, McDougall & Stipp 1968), in which case, the Mount Rouse eruption would fall almost precisely on the boundary. Recent authors (e.g. Harland *et al.* 1982, Veevers 1984) place the boundary at 2.0 million years. Despite this slight change, the Mount Rouse eruption falls sufficiently close to the boundary to provide a very convenient marker between the Quaternary and Tertiary flows. Quaternary flows retain topographic features such as stony rises: older flows do not.

The potassium-argon date comes from within the cone, and it might be argued that the cone is much younger than the underlying flows. But in the next section it is argued that the whole volcanic eruption probably took place very quickly, and the age indicated can be regarded as also the age of the underlying lava flows. If this is so there is still a problem of the younger date of McDougall and Gill (1975) listed above. Either their dates are too young, or my 1.82 m.y. date is too old, or there are several different flows. The last possibility seems very unlikely because of the continuity of the very distinctive flows, as seen in the field and on air photographs.

Gill (1957) and Gibbons and Gill (1964) suggested that the basalt of the Hamilton Land-system can be relatively dated at Grange Burn, where basalt overlies fossiliferous marine Kalimnan (Lower Pliocene) on which a palaeosol had developed before the basalt cover was erupted. The basalt was later dated (Turnbull *et al.* 1965) and gave a potassium-argon age of 4.35 ± 0.10 m.y. (4.46 ± 0.10 m.y. on new decay constants). Another date for the Hamilton Land-system basalt was reported by McDougall *et al.* (1966), from Menzel's Quarry, Penshurst, as 3.91 ± 0.15 m.y. (4.01 ± 0.15 m.y. on new decay constants). The Hamilton Land-system basalt therefore had something like 2 to 2.5 million years of weathering before basalt was erupted from Mount Rouse. The Pliocene climate was wetter and warmer than the average Quaternary climate, and the age difference is probably quite enough to explain the very different degrees of weathering.

THE FORMATION OF VERY LONG LAVA FLOWS

The features of the lava flows from Mount Rouse have a bearing on modern ideas about the formation of very long flows, and the nature of the mechanism by which lava flows. Walker (1973) analysed the factors affecting the length of lava flows. He believed that viscosity merely controls the thickness of a lava extrusion, and only indirectly affects the length. The

effect of the angle of slope of the underlying land surface, though not negligible, is small in relation to other factors.

This must certainly be so at Mount Rouse, for it flowed over very low gradients. The overall gradient from cone to sea is 1 in 200 (300 m in 60 km), but the more distal portions are considerably flatter.

Walker concluded that the major factor affecting the length of a lava flow is the effusion rate, especially the effusion rate over the first few days of eruption, which is higher than the average rate.

Malin (1980) examined the length, volume and effusion rate of 87 historic Hawaiian lava flows, and found there was little support for a direct relationship between flow length and effusion rate. A relationship between flow length and total volume extruded is statistically more significant. He noted that cross sectional area, effusion rate and volume all play important roles in governing the emplacement of flows and stated "One reason for the observed relationship in Hawaii may be that tube-fed flows, with approximately constant cross-sectional area, advance farther than other types of flows for similar effusion rates and volumes."

Effusion rate may be less important than the continuity of flow in time. If an eruption ceases just long enough for the lava to solidify, lava tubes will be blocked. Lava from a subsequent eruption will then flow *over* the earlier flow, increasing its thickness but not its length. If, on the other hand, an equivalent volume of lava was erupted without interruption, a single very long flow is more likely to be produced, with a lava tube system operating for a longer period.

Flow morphology of lava must be related in some way to its rheological properties. Above the liquidus a silicate melt behaves as a Newtonian fluid (a simple fluid in which the state of stress at any point is proportional to the time rate of strain at that point), but since the classic work of Shaw *et al.* (1968), lava has generally been treated as a Bingham plastic (a non-Newtonian fluid exhibiting a yield stress which must be exceeded before flow starts). Hulme (1974) showed both theoretically and experimentally (using flows of kaolin and water) that flowing Bingham fluids form stationary bodies of fluid at the margins of a flow and have a characteristic thickness for a given slope. In a lava flow, levees of stationary lava might be formed on each side of a mobile flow. This was observed on Mt Etna by Sparks, Pinkerton and Hulme (1976) who wrote "As Hulme predicted, two bordering zones of stationary incandescent lava were formed, termed "initial levees", which determine the width of the channel". It must be remembered that Hulme's hypothesis has limitations, for it is derived for flows in which cooling plays no part.

Fig. 4 (top)—Stereo air photos of Mount Rouse. Note the mound built of stony rise lava on which the final scoria cone was built. Scale 1: 80 000.

Fig. 5 (bottom)—Stereo air photos of the Moorilah Steptoe and the flows which surround it. Note the surface features of the stony rises, and the way lava flows up even minor tributaries. Scale 1:80 000. These photographs are Crown Copyright and have been reproduced by permission of the Director, Division of National Mapping, Department of Resources and Energy, Canberra, Australia.

Very long flows probably cannot be maintained by the "central channel and levee" mechanism. Wilson and Head (1983) wrote "In some cases the upper surface of a flow becomes rigid long before the interior and motion takes place in an enclosed (and hence thermally insulated) tube within the body of the flow." Wadge (1978) had already concluded that "Flow will cease when the chilled crusts develop to some critical thickness." Swanson (1973), however, indicated that lavas within tubes flowed virtually isothermally, cooling at a rate of only about $1^{\circ}\text{C.km}^{-1}$. Malin (1980) suggests that such tube-fed flows, if limited only by cooling, could possibly produce flows up to 200 km long, a mechanism quite adequate for the 60 km Mount Rouse flow.

The Mount Rouse flow indicates by its length and its stony-rises morphology that it was a tube fed flow, and was emplaced by mechanisms similar to those described by Wadge, Swanson and Malin. If this is so, it was probably emplaced in a relatively short time, perhaps only days or weeks. The fluidity of the lava flows is further indicated by the apparent ease with which the lava divided into several different flows which re-united further downstream after they had flowed around obstacles. In relation to the lava levee observations of Sparks, Pinkerton and Hulme (1976), it is important in Victoria to distinguish between levees and lateral ridges. Examples of levees can be seen in Victoria where flows leave the northern end of Lake Surprise in the crater of Mount Eccles, and also from Little Mount Eccles. They are essentially formed only close to the point of eruption. Lateral ridges, also called "pressure ridges" in Victoria (Skeats & James, 1937), are found farther down-flow and result from collapse of the flow surface, not from build-up like a levee. In the Mount Rouse flow there are no lava levees, but lateral ridges are occasionally present.

SUMMARY

Mount Rouse erupted about 1.8 million years ago. Eruption of lava flows probably lasted for only a few weeks during which flows covered the 60 km to the sea. Eruption of the Mount Rouse cones and craters was more complicated, and probably lasted somewhat longer. The lava flows were tube-fed, which accounts for the hummocky stony rises topography which is still largely intact. Weathering and erosion are very limited.

For many years the Cainozoic basalts of Victoria have been divided into the Older Basalts and the Newer Basalts. The Newer Basalts can now be divided into two sets, and Mount Rouse marks the beginning of the youngest set (which might be conveniently called the Quaternary Basalts). These include the Giringurrup and younger Land-systems of Downes, Gibbons and Gill. The earlier set of Newer Basalts, including those of the Hamilton Land-system has very much more weathering, although it is not very much older. This might be the result of a considerable climatic change in Victoria before the Quaternary flows were erupted.

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FIRST RECORD OF WELL-PRESERVED MEGAFOSSILS OF *NOTHOFAGUS* FROM MAINLAND AUSTRALIA

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ABSTRACT: Mummified leaves, cupules and seeds of *Nothofagus* (Fagaceae) have been recovered from the Miocene Bacchus Marsh Locality in Victoria, Australia. Preliminary numerical analysis of the leaves suggests one diverse species present with no close similarities to any extant Australian species of *Nothofagus*. Also no strong similarities are initially apparent to any of the fossil species recently described from Tasmania. Both leaves and cupules support assignment of the fossils to either section *Calusparassus* or section *Nothofagus* subsection *Quadripartite* of *Nothofagus*.

Biogeographic considerations of Gondwanaland frequently include discussions of *Nothofagus* (Raven & Axelrod 1972, van Stennis 1972, Cracraft 1975, Schuster 1976, Humphries 1981). These discussions are usually based on distribution of extant species, as the fossil record of the genus — particularly the megafossil record — has been far from adequate. These discussions have therefore rarely brought forward definitive solutions to the problems of evolution and radiation of species within the genus. Australia has been particularly perplexing in this regard in that while a diverse, and indeed frequently dominant, fossil pollen record for *Nothofagus* in the Tertiary is known (Kemp 1978, Martin 1982), no confirming megafossil evidence had been forthcoming (Christophel & Blackburn 1978). Megafossil remains of *Nothofagus* have been recently described from Tasmania (Hill 1983 a, b, 1984), but prior to this report, no organically-preserved megafossil remains were known from continental Australia. Some fossils of *Nothofagus* have been reported from continental Australia in the past (e.g. Paterson 1935) but in all cases cuticular remains were either not present or not reported. Coupled with the fact that the fossils in many of these reports were found in coarse sediments where venation detail is not preserved well, the identification of those fossils must remain questionable.

LOCALITY

The fossils described in this report were collected in early 1984 from the overburden at the Maddingley Coal Mine in Bacchus Marsh, Victoria, Australia (37°41'S, 144°36'E). The leaves and fruits occur as part of a grey-brown carbonaceous clay lens occurring 2 m above the surface of the coal seam. This coal seam is considered to be a part of the Tertiary Werribee Formation (Abele 1976, Roberts 1984).

The palynoflora of the clay lens has been identified as belonging to the *Triplopollentites bellus* zone of Stover and Partridge (1973) by A. Partridge, Esso of Australia (pers. comm.), based on the frequency of *T. bellus*. While this zone was originally considered to be Middle to Late Miocene, foraminiferal evidence from

the Murray Basin indicates an Early Miocene age for it (W.K. Harris, Western Mining Corp., pers. comm.). This dating places the Bacchus Marsh clay in the same zone as the Yallourn Clay of the Latrobe Valley coal system (Luly, Sluiter & Kershaw 1980).

MATERIALS AND METHODS

The mummified leaves and fruits were recovered by macerating blocks of the clay in hot 20% W/V H₂O₂ and sieving the resultant slurry. In this manner over 150 mummified leaves and fruits were recovered. The commonest leaf type is a simple, serrate, craspedodromous angiosperm which, based on venation, stomatal arrangement and trichome types was readily assignable to *Nothofagus* (Fig. 1a). The dominant fruit type recovered was a four parted cupule, occasionally complete with three seeds, which was also readily assignable to *Nothofagus* (Fig. 1b). The 24 most complete fossil leaves were selected for morphological examination. These leaves have a large range of lengths (1.2-5.1 cm) with several fragmentary specimens having a projected length of greater than 7 cm. Seven leaves had lengths very near the minimum, giving a significant difference between the mean and median length values. This size distribution might be interpreted as more than one species present, or a number of juvenile leaves in the sample, or reproductive leaf dimorphism such as that demonstrated by Hill for *Nothofagus moorei* (Hill 1983b).

A preliminary numerical analysis of the leaves, and leaves from 11 extant species of *Nothofagus* from section *Nothofagus* and section *Calusparassus* subsection *Quadripartite* was carried out using many of the characters proposed by Hill (1983a) and the distance metric of Blackburn (1980). A list of the characters used is presented in Table 1. Most were taken directly from Hill's analysis of *Nothofagus* (1983a) but several were slightly modified to provide cut-off points for character states more consistent with the current data set. Several of Hill's characters were omitted because the OTUs for this analysis did not display features used in his analysis. Specifically the Type Three trichome of Hill was not

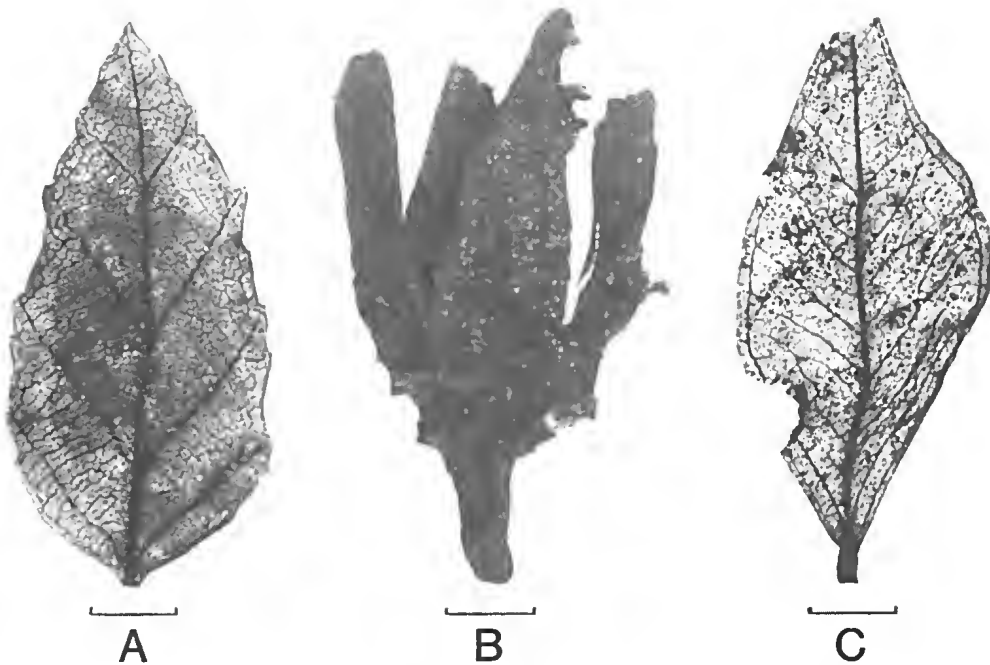


Fig. 1—Megafofssils from Bacehus Marsh, Australia. A, Fossil leaf of *Nothofagus* showing craspedodromous secondary venation and pcreurrent tertiary venation. Scale bar equals 4 mm. B, Fossil fruit cupule of *Nothofagus* showing four parts. Scale bar equals 1.7 mm. C, Fossil Myrtaceous leaf. Scale bar equals 3.5 mm.

present in the Bacehus Marsh fossils or in the extant species included, and hence characters relating to them were dropped. A dendrogram was then constructed using the UPGMA clustering algorithm (Fig. 2). Leaves of extant species from section *Calusparassus* subsections *Bipartite* and *Tripartite* were omitted from the analysis as all leaves were obviously toothed, all the cupules were four parted and they contained three seeds.

RESULTS AND DISCUSSION

While the preliminary nature of this analysis must be emphasised, several observations may be made from the results (Fig. 2). Firstly it may be seen that 22 of the 24 fossils cluster together (or at least are more similar to each other than to leaves of any extant species included). By observing the relative level at which the dimorphic leaves of *Nothofagus moorei* clustered, it becomes

TABLE 1

CHARACTERS SCORED FOR EXTANT AND FOSSIL OF LEAVES *Nothofagus*. STATE 1 OF EACH CHARACTER IS EXPRESSED IN THE TABLE. CHARACTERS WITH AN ASTERISK ARE FROM HILL (1983a).

*	1. Adaxial glandular trichome bases present
*	2. Adaxial non glandular trichome base present
*	3. Abaxial glandular trichome bases present
*	4. Abaxial non glandular trichome bases present
*	5. Giant stomates present
*	6. Subsidiary cells irregularly thickened
*	7. Abaxial epidermal cells convoluted walls
*	8. Less than 12 secondary veins (pairs)
*	9. Secondary veins straight for greater than or equal to $\frac{2}{3}$ of length
	10. Secondary vein angle of divergence from primary vein 45°
*	11. Intersecondary veins present
*	12. Tertiary veins pcreurrent, oblique, convex
*	13. Serrations glandular or spinose
*	14. Serrations only in upper $\frac{1}{2}$ - $\frac{1}{3}$
*	15. Tooth sinus angular
	16. Principal tooth vein ramified
*	17. Serrations 2 per secondary vein interval
*	18. Leaf length less than 4 cm.

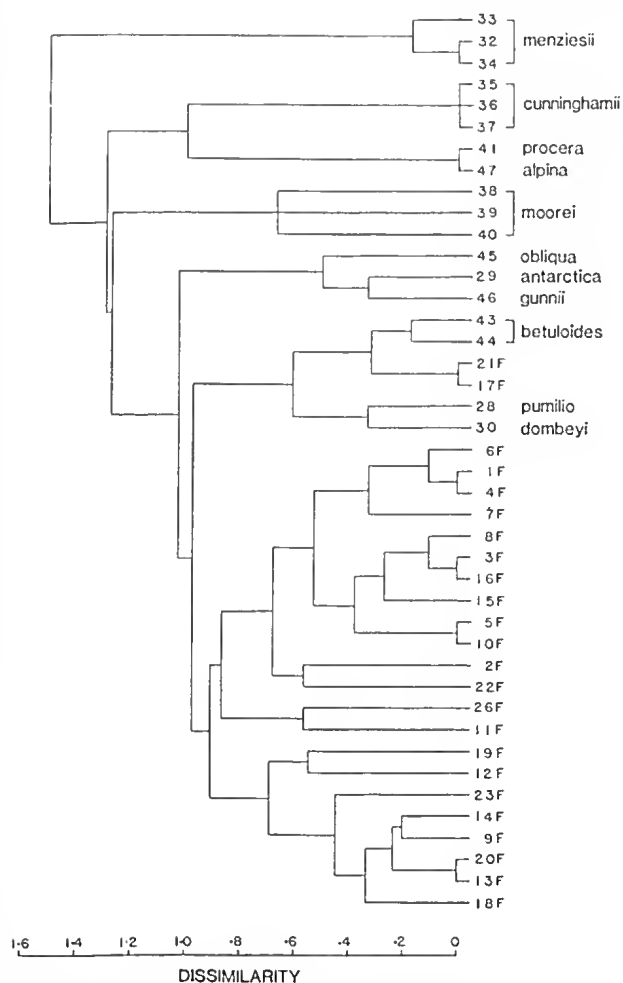


Fig. 2—UPGMA dendrogram of the 11 extant species and 24 fossil specimens of *Nothofagus*. Each number on the vertical axis (OTU's) represents one leaf. A number followed by an "F" represents fossil leaves from Bacchus Marsh, Victoria.

reasonable to interpret the 22 as a single variable taxon. The two remaining fossil leaves (Fig. 2 — 17F and 21F) cluster most closely with the South American *Nothofagus betuloides*. The significance of this may be diluted by the fact that these two fossil specimens are missing their lamina bases, and hence several characters were unscored for them. A final observation from Fig. 2 is that the three Australian species, *N. moorei*, *N. cunninghamii* and *N. gunnii*, show no great similarity to the Bacchus Marsh fossils. Clearly an additional analysis incorporating more specimens of some extant species and also including several extant species which had not been available for this analysis is indicated before definite conclusions on the relationships of the Bacchus Marsh fossils can be made.

A non-numerical comparison with the fossil species described by Hill from Tasmania deposits (1983a, b, 1984) based on their published descriptions was also undertaken. These fossils were not included in the numerical analysis because data on individual leaves

from those taxa were not available and it was considered undesirable to include an aggregate OTU with a set in which all others were individual leaves. Using architectural features, the lack of a fimbrial vein and the size variability displayed by the Bacchus Marsh fossils make them most similar to *Nothofagus johnstonii* Hill. However, the tooth/secondary vein ratio of 2.0 for the Bacchus Marsh fossils, as well as several other architectural features differ from the descriptions of *N. johnstonii*.

The cuticular features of the Bacchus Marsh fossils are also different from those described for the Tasmanian fossil *Nothofagus*. The Bacchus Marsh fossils have the typical cycloctytic arrangement of subsidiary cells, but unlike *Nothofagus johnstonii* Hill and *N. tasmanica* Hill, they do not exhibit pronounced cuticular thickenings on the subsidiary cells. Of the trichome types described by Hill (1983a), the complex glandular trichome and the non-glandular type with a heavily-cutinized circular foot cell and a simple hair are both commonly found on abaxial and adaxial surfaces of the Bacchus Marsh fossils. The non-glandular type is particularly dense on the adaxial (non-stomatal) surface over veins and the margin. The other trichome types described by Hill have not been observed on the Bacchus Marsh fossils on either leaf surface. This combination of epidermal features does not match particularly well with any of the fossil Tasmanian species.

As only a solitary cupule from one Tasmanian fossil species has been described to date, and as cupules of several of the relevant extant species have yet to be obtained, no comparisons for the fruits are made. Seeds recovered from the Bacchus Marsh deposit are not preserved sufficiently well for comparisons to be made with extant material.

The overall diversity of the megafossil flora at Bacchus Marsh is relatively low. The second commonest leaf type has affinities with the Myrtaceae (Fig. 1c). Two angiosperm leaf types of unknown affinities have also been recovered, as well as one Araucariaceae twig and several leaves presumed to belong to the Podocarpaceae. Two other fruit types also commonly occur in the deposit, but they have not yet been identified.

Despite the apparent dissimilarity of the *Nothofagus* leaves, the remainder of the Bacchus Marsh flora has elements in common with the Tasmanian Pioneer flora of a similar age. The Pioneer flora is also of a reasonable low diversity, has several coniferous taxa and Myrtaceae leaves are also represented (Hill & Macphail 1983). These same elements are also present in the Miocene Yallourn deposit of Victoria, although *Nothofagus* megafossils have not been reported from that locality.

The discovery of abundant organically-preserved *Nothofagus* megafossils at the Bacchus Marsh locality provides the first supportive evidence from mainland Australia for the "*Nothofagus* flora" which the palynological record has suggested was dominant in the Tertiary. The predominance of microphyllous leaves and the low diversity of the flora are consistent with a cool-temperate forest vegetation. Such a vegetation type

could alternatively be found, however, at a higher altitude in a slightly warmer temperate region. Hill (1983) suggested that information about fossil *Nothofagus* on mainland Australia was crucial to the study of evolution within the genus. The discovery of the Baecheus Marsh flora with its abundant *Nothofagus* remains should therefore aid in the continuance of evolutionary studies within the genus and provide additional data with which to test some of the relationships between taxa hypothesized by Hill (1983, 1984).

As more and more records of *Nothofagus* megafossils become documented, perhaps the statement of Patterson (1980) that "*Nothofagus* is uninformative on the interrelationships of the southern hemisphere areas" can ultimately be challenged.

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THE GENUS *EUDENDRIUM* (HYDROZOA: HYDROIDA) FROM AUSTRALIA

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ABSTRACT: Seventeen species of *Eudendrium*, including ten newly described, are reported from Australia. All known Australian material of *Eudendrium* has been examined in this study and past misidentifications rectified. Five species: *E. ramosum* (Linnaeus, 1758); *E. racemosum* Cavolini, 1785; *E. capillare* Alder, 1856; *E. carneum* Clarke, 1882; and, *E. glomeratum*, Picard, 1951 are new records for Australia. Two tropical species, *E. kirkpatricki* n. sp. and *E. infundibuliforme* Kirkpatrick, 1890, are recorded from Torres Strait and Papua New Guinea. The former also ranges from the north of Western Australia to the Great Barrier Reef while the latter is now recorded from several places on the Great Barrier Reef. *Eudendrium terranova* n. sp., formerly recorded from northern New Zealand as *E. novaezealandiae* Marktanner-Turneretscher, 1890, is now reported from southern Australia. *Eudendrium pusillum*, von Lendenfeld, 1885 is synonymised in *E. generale* von Lendenfeld, 1885 and the range of *E. generale* is now reduced to temperate south-eastern Australia.

The importance of the endome in classification of the Eudendriidae is discussed and the genus *Eudendrium* is redefined by including features of the endome in the diagnosis. A key is given to the Australian species of *Eudendrium*.

This paper extends knowledge of the distribution of the *Eudendrium* fauna around Australia. Most of the species are recorded from the eastern and south-eastern coastline; only four are known from Western Australia and none from the Northern Territory, Tasmania or the Great Australian Bight. Present records indicate a highly endemic *Eudendrium* fauna with species confined mainly to one or two marine biogeographic provinces. Only *E. aylingae* n. sp. is recorded from three provinces, ranging from cool temperate to tropical waters.

Previous records of *Eudendrium* from Australia include: an unidentified species (Bale 1884); *Eudendrium generale* von Lendenfeld, 1885; *E. pusillum* von Lendenfeld, 1885 (= *E. lendenfeldi* Briggs, 1922 and *E. indopacificum* Stechow, 1923); *E. capillare* Alder, 1856; *E. album* Nutting, 1898; and, *E. infundibuliforme* Kirkpatrick, 1890. Species originally described from Australia include: *E. generale*, recorded from the south coast (von Lendenfeld 1885, Bale 1919) and the tropical north in Torres Strait (Kirkpatrick 1890, Pennycuik 1959); and, *E. pusillum*, from the temperate eastern coastline (von Lendenfeld 1885, Ritchie 1911) and from tropical north-western Australia (Jäderholm 1916) *Eudendrium infundibuliforme* has been recorded only once, from Torres Strait (Kirkpatrick 1890, Pennycuik 1959); *E. capillare* was reported from the tropical east coast (Pennycuik 1959) and the subtropical west coast (Stechow 1925); and, *E. album*, from the tropical east coast (Pennycuik 1959).

In the course of the author's subtidal ecological studies in southern Australia it became necessary to distinguish between some commonly-occurring species of *Eudendrium*. This requirement led to a critical reappraisal of type material, examination of all known Australian material, some New Zealand specimens, and material held in the personal collection of the author. This investigation has revealed misidentification of some species, for example, *E. generale* of Kirkpatrick (1890), Bale (1919) and Ritchie (1910), and *E. capillare* of Stechow (1925) and Pennycuik (1959). Re-examination

of von Lendenfeld's type material of *E. generale* and *E. pusillum* leads to the conclusion that the latter (and thus, *E. lendenfeldi* Briggs, 1922 and *E. indopacificum* Stechow, 1923) are synonyms of *E. generale*.

On the basis of this review, the family Eudendriidae in Australia now comprises 17 species, ten of which are here described as new. It is accepted here that some of the newly-described species, particularly those of the "*E. capillare*" group, whose taxonomy is in need of critical world-wide revision, might eventually be synonymised with that species. *Eudendrium generale* of Kirkpatrick (1890) and *E. capillare* of Stechow (1925), are considered to be a new species with a wide distribution through the tropical north of Australia. *Eudendrium generale* of Bale (1919) proves to be an undescribed species, while *E. infundibuliforme* Kirkpatrick, 1890, an easily-identifiable hydroid, is now shown to have a wide distribution from Papua New Guinea through the length of the Great Barrier Reef. Earlier records of *E. capillare* have been found to be incorrect and the species is now doubtfully recorded from only two localities in eastern Australia. Species known from outside the Australian region include: *E. ramosum* (Linnaeus, 1758); *E. racemosum* Cavolini, 1785; *E. capillare* Alder, 1856; *E. carneum* Clarke, 1882; and, *E. glomeratum* Picard, 1951. With the exception of the latter, all are well known, widely-distributed species, while *E. capillare* is near cosmopolitan. The Australian record of *E. glomeratum* is the first for that species outside the European region.

The search for identity of Australian species also led to the comparison of the type material of *Eudendrium novaezelandiae* Marktanner-Turneretscher, 1890 from New Zealand with the "Terra Nova" specimen doubtfully assigned by Totton (1930) to this species. Totton's specimen, which is identical with abundant material collected by the author in Bass Strait, Victoria, is not *E. novaezelandiae*, but a species here described as new. A redescription of *E. novaezelandiae* will be given elsewhere (Watson in prep.).

The family Eudendriidae has long been one of the more diagnostically troublesome of the Athecata. Many authors (e.g. Nutting 1898, Totton 1930, Vervoort 1959, 1972, Millard 1975) have acknowledged problems in distinguishing between the species of *Eudendrium* because of similarity of colony morphology throughout the genus. Fraser (1912) correctly pointed out that branching and colony height are not specifically constant features; nevertheless, he considered sexual differences to be adequate to distinguish between his North American species. Unfortunately, the reproductive structures show remarkably little morphological variation throughout the genus. The male gonophores in various species are one to four chambered, arising in a verticil below a hydranth which may remain fully developed, or show varying degrees of atrophication. Similarly, the female gonophores are borne on a blastostyle which may show some, or no atrophication of the tentacles, or may simply have a reduction in the number of tentacles present. The female spadix is usually unbranched and is resorbed as the single egg approaches maturity. A few species (such as *E. carneum* Clarke, 1882; *E. racemosum* Cavolini, 1785; *E. ritchei* Millard, 1975; and, *E. motzkossowskiae* Picard, 1951) have a branched female spadix and are more readily identifiable than most species of *Eudendrium*. Thus, considered alone, the reproductive structures can give no more than a guide to the identity of species. However, when considered in conjunction with features of the cnidome, they usually provide a good guide for identification of species (Werner 1965).

THE CNIDOME IN CLASSIFICATION

The systematic importance of the cnidome of *Eudendrium* has received surprisingly little attention. Early workers noted the presence of nematocysts in the hydranth—the "thread cells", "gland cells" and "nettle ring" (Hincks 1868, Allman 1871, von Lendenfeld 1885, Kirkpatrick 1890), and nematocyst pads associated with the gonophores (Bale 1919). Light (1913) described, and gave dimensions of, the nematocysts in *E. griffini* (= *Myrionema griffini*) from the Philippines. Broch (1916) noted, but did not explore the diagnostic value of, the "rod-shaped" nematocysts in the tentacles, and the different, much larger "basal capsules" in the hydranth of *E. wrighti* Hartlaub, 1905. Weill's (1934) classic study on the morphology, physiology and development of nematocysts, including those of *E. racemosum*, provide a foundation that has been follow-

ed by Picard (1951, 1955), Werner (1965) and Millard (1975) for identification of species of *Eudendrium*.

Details of the cnidome are known for about one-third of the known species of *Eudendrium* (Bouillon pers. comm., Mergner pers. comm., Weill 1934, Itô & Inoue 1962, Millard & Bouillon 1974, Cooke 1975, Millard 1975, Kubota 1976, Rösler 1978). Millard (1975) used kind and shape of nematocysts, in conjunction with other colony characters, to key out southern African species of *Eudendrium*.

In the present study, the nematocysts and the cnidome are used as a primary systematic tool for distinguishing between the Australian species of *Eudendrium*. The classification of nematocysts by Weill (1934), Werner (1965) and Mariscal (1974), adopted here, provides a satisfactory, if somewhat detailed, basis for identification. Nonetheless, problems of specific identity sometimes still occur, due to the difficulty of correctly identifying incompletely-discharged or undischarged nematocysts.

Members of the genus *Eudendrium* are related in the possession of small microbasic euryteles in the tentacles. The pyriform capsule of the tentacular nematocysts may range in size from 5 to 10 μm in length and 2 to 4 μm in width. The shaft is usually 1 to 2 μm shorter than the capsule, and bears a few distal spines. The shaft discharges forward in the long axis of the capsule and the thread is usually fine and moderately long. The tentacular nematocysts of some Australian species have a thicker thread with fine, but distinct, bristles. Because of their similarity throughout the genus, the tentacular microbasic euryteles are not especially useful in identification of species.

When nematocysts of more than one size or kind are present, they are collectively designated as the cnidome. The supplementary nematocysts of the cnidome never reside in the tentacles but are situated around the hypostome or on the body of the hydranth. In some species they are scattered on the spadix of the female gonophore or aggregated into distal pads on the gonophores of either sex. With few exceptions, the larger microbasic euryteles situated around the hypostome discharge sideways, probably to allow the thread to eject laterally across the mouth. The shaft itself may also be penetrant and capable of restraining prey, since the distal end is often heavily armed with bristles and spines. This armature is often distinctive enough to be specifically diagnostic. The armature of some species, e.g. *E. capillare*, and several species described here as new, comprises only small, forwardly-discharging microbasic euryteles similar to those in the tentacles. Laboratory observations on living material of a species possessing only small microbasic euryteles showed that the hydranths have a very reactive hypostome suggesting that this species may compensate for a weak armature by placing more reliance upon rapid engulfment, rather than entanglement, of prey.

Five of the species recorded here have only microbasic euryteles in the cnidome; eleven species have two kinds, and one species has three kinds of

nematocysts. Although the cnidome is usually constant in the kind and abundance of its constituent nematocysts to be diagnostically useful, some species noted in this study, for example, *E. infundibuliforme* Kirkpatrick, 1890, and *E. generale* von Lendenfeld, 1885 possess "fugitive" nematocysts which may be common to rare, or possibly, absent altogether. Loss of nematocysts without replacement, as shown by *E. generale*, may lead to problems in identification, since sterile specimens of this species, lacking supplementary microbasic euryteles, can be easily confused with *E. capillare*. It is possible that gradual attrition of the cnidome through ageing of the colony may not be especially rare among the Eudendriidae. Further critical study of this phenomenon is warranted in view of the taxonomic implications.

Five species (30% of the Australian *Eudendrium* fauna) have a cnidome including large microbasic euryteles additional to the small tentacular microbasic euryteles. Seven species have kinds of nematocysts other than microbasic euryteles. Five of these have heteronemes and two species have haplonemes. One of the heteronemes is identified here as a microbasic p-mastigophore, in a species newly described from southern Australia. Although the other heteronemes are here classified as macrobasic euryteles, identification is somewhat doubtful in cases where there are no discharged nematocysts in the material available for examination.

Apart from variations in relative abundance, the size of the nematocysts comprising the cnidome may also vary within and between colonies of the one species, as well as over the geographic range of the species. Regional differences in size of nematocysts are exemplified by the difference in size of the larger microbasic euryteles of *E. ramosum* being 50% greater in Australian specimens than in those from southern Africa (Millard 1975) and the Mediterranean Sea (Mergner pers. comm.). Despite such variations in absolute size of nematocysts, the length to width ratio of the capsule (Kubota 1976) is usually relatively constant. This ratio has therefore been adopted in this study as an aid to identification of species.

Although requiring further study to determine the limits of variability of form and size within each species, nematocyst morphology will become an increasingly useful diagnostic tool in future taxonomy of many athecate groups. Critical world revision of the Eudendriidae using electron microscopy of nematocysts after the manner demonstrated by Mergner and Wedler (1977) and Östman (1979) will provide a better understanding of the variability of the cnidome, and hence, of species.

EXAMINATION OF THE CNIDOME

Whenever possible, fresh, living material collected using SCUBA was used in this study. Specimens were placed individually in plastic bags and sealed underwater to reduce the likelihood of contamination by foreign nematocysts.

Good to excellent discharge of nematocysts could usually be achieved on mounting a living specimen directly into Berlese medium (Mahoney 1973). Similarly, specimens preserved in alcohol may be discharged satisfactorily in this, or other aqueous mountants, but discharge cannot be induced in formalin-preserved material. Drying and re-hydrating and other methods using various reagents, such as dilute acids and alkalis (Yanagita & Wada 1953), were not always successful in discharging certain kinds of nematocysts, even in fresh material. Discharge of even the most resistant nematocysts can be achieved by immersion of the specimen in a dilute solution of domestic bleach (4% Cl_2 M/V) for 30–60 sec, washing in fresh water, then mounting directly into an aqueous medium. This treatment may, however, cause delicate threads to detach or even dissolve.

Russell (1938) has pointed out that confident diagnosis of nematocysts requires examination of an extensive range of material. It was found in the present study, that examination of several hydranths, hydranth pedicels and thin-walled parts of branches and gonophores, preferably from several colonies, was necessary for satisfactory examination of the cnidome. Specimens were first examined whole in the mountant to determine disposition of the nematocysts, then squashed for examination ($\times 1,000$, oil immersion lens, using phase contrast). To reduce inaccuracies in dimensions only nematocysts seen in full in lateral view were measured.

Migration of the cnidoblast has been studied in *Tubularia* (Hadzi 1907) and the mechanism of exchange in *Hydra* (Semal-Van Gansen 1951, Burnett & Lentz 1960). The only detailed observations on nematocyst migration in *Eudendrium* are by Mergner (1957) who examined this phenomenon in *E. racemosum*. The coenosarc of pedicels and branches of Eudendriidae often contain many undischarged nematocysts in transit between various parts of the colony. When the colony consists only of bare stems, as often occurs with moribund or poorly-preserved specimens, study of transitory nematocysts can provide a useful means of identification of species. Examination of nematocysts enclosed within the perisarc has the added advantage that adventitious nematocysts from other cnidarians are excluded, thus allowing more confident diagnosis.

REPRODUCTIVE STRUCTURES

Most descriptions of the reproductive structures of *Eudendrium* refer merely to presence or absence, or partial to complete atrophy of the tentacles of the hydranth or the blastostyle. Examination of the large amount of fertile material in the present collection shows that considerable information can be gained at the specific level by detailed investigation of the morphology of the blastostyle. For example, in some species there are no tentacles present on the blastostyle even at the earliest growth stage of the gonophores; in other species a full complement of tentacles may surround a fully-developed hydranth throughout maturation. In-

intermediate patterns, such as retention of normal tentacles with or without loss of the hypostome occur in some species, while others may show a reduction in the size or the number of tentacles present. Reduction in the number of tentacles often occurs through a process of selective atrophy or complete resorption of alternate tentacles (see electron micrograph of *E. ramosum* by Rösler 1978, Pl. 39, Fig. 2). Such strategies may have developed to relieve overcrowding of the hydranth in species which bear a large number of female gonophores on the body of the hydranth.

Wherever possible in this paper, the reproductive structures are described in detail, preferably from a growth series of living or freshly-preserved material.

MATERIAL

Type and other material examined in this study has originated from, or has been lodged in the British Museum (Natural History) (BM), the Queensland Museum (QMGL), the Australian Museum (AMG), the Museum of Victoria (MVF) and the Western Australian Museum (WAM). Some material is also held in the personal collection of the author.

SYSTEMATICS

Family EUDENDRIIDAE

The Family Eudendriidae comprises only two genera, *Eudendrium* and *Myrionema*. The latter is a rare genus, distinguished from *Eudendrium* by the large number of tentacles in several close whorls on the hydranth. It has been recorded once from Australia as *Myrionema amboinense* Pictet, 1893 by Briggs and Gardner (1931). The original definition of the genus *Eudendrium* by Ehrenberg (1834) has been changed by successive authors (Hincks 1868, Allman 1871, Hartlaub 1905, Mergner 1957, Naumov 1960, Millard 1975, Stepanjants 1979). It is here further modified by the additional description of the kind of nematocyst common to all species of the genus.

Genus *Eudendrium* Ehrenberg, 1834

DIAGNOSIS: Hydrocaulus invested with perisarc. Hydranths radially symmetrical with large hypostome and a whorl of filiform tentacles. Microbasic euryteles always present in tentacles; other kinds of nematocysts may be present in hydranth and gonophores. Gonophores, fixed sporosacs, borne on hydranth below tentacles. Reproductive hydranth often reduced to a blastostyle. Male gonophores single or in linear series. Young female gonophore a single egg encircled by a spadix.

KEY TO THE SPECIES OF *EUDENDRIUM* FROM AUSTRALIA

Numbers in brackets refer to the order in text and to the distribution map (Fig. 95).

1. Nematocysts comprising all microbasic euryteles. 2
 - Cnidome includes nematocysts other than microbasic euryteles 11
2. Microbasic euryteles all of same size 4
 - Microbasic euryteles not all of same size 3
3. Microbasic euryteles of two sizes present 8
 - Microbasic euryteles of three sizes present *E. minutum* (1)
4. Colonies of medium size (to 100 mm height), stems fascicled, branching orderly 7
 - Colonies small (to 25 mm height), stems unfascicled, irregularly branched 5
5. Mature male gonophore on hydranth with fully developed tentacles *E. pennycuikae* (2)
 - Mature male gonophore on blastostyle entirely devoid of tentacles 6
6. Nematocyst pads present on gonophores of both sexes *E. nambuccense* (3)
 - No nematocyst pads on gonophore.. *E. capillare* (4)
7. Pedicel of hydranth indistinctly annulated *E. terranova* (5)
 - Pedicel of hydranth deeply corrugated throughout *E. corrugatum* (6)
8. Mature gonophores of one or both sexes on hydranth with full number of tentacles 9
 - Mature gonophores of both sexes on blastostyle without tentacles 10
9. Mature gonophores of both sexes with tentacles reduced to stumps *E. ramosum* (7)
 - Mature female gonophore on blastostyle without tentacles *E. kirkpatricki* (8)
10. Supplementary nematocysts of cnidome with a few spines on shaft *E. generale* (9)
 - Supplementary nematocysts of cnidome with numerous bristles on shaft *E. merulum* (10)
11. Cnidome with haplonemes 12
 - Cnidome with heteronemes 13
12. Cnidome includes heterotrichous anisorhizas; mature female gonophore enclosed in a fenestrated capsule, *E. carneum* (11)
 - Cnidome includes atrichous isorhizas; cnidophores sometimes present *E. racemosum* (12)
13. Cnidome includes macrobasic euryteles 14
 - Cnidome includes nematocysts other than macrobasic euryteles: microbasic mastigophores present *E. balei* (13)
14. Colonies of moderate size, up to 80 mm in height.. 16
 - Colonies small, up to 12 mm in height 15
15. Macrobasic euryteles elongate, paddle-shaped, length-width ratio 3:1, shaft with overlapping spines, *E. aylingae* (14)
 - Macrobasic euryteles oval in shape, length-width ratio 2:1, shaft very long *E. currumbense* (15)
16. Pedicel of hydranth expanding distally *E. infundibuliforme* (16)
 - Pedicel of hydranth of same diameter throughout, nematocyst pads on lower body of hydranth *E. glomeratum* (17)

Eudendrium minutum n. sp.

Figs 1-4

TYPE MATERIAL AND RECORD: Holotype MVF50520, one colony alcohol preserved, on dead stem of aleyonarian *Mopsea encrinura* (Lamarck), depth 12 m, Port Phillip Heads, Victoria, 38° 18' S, 144° 40' E; coll: J. E. Watson (SCUBA), 13/12/82.

DESCRIPTION OF HOLOTYPE: Colony sterile, comprising 15-20 stems arising from a tubular stolon wandering on surface of substrate. Stems up to 3 mm in height, unfascicled, slender, simple, or if branched, bearing 1-3 irregularly-spaced branches each with a terminal hydranth. Lower part of branched stems and simple stems deeply annulated with up to 10 spiral rings, branches with a few indefinite proximal annulations, those terminating in a hydranth frequently annulated throughout. Perisarc of stems moderately thick, becoming thinner distally. Hydranths small, with approximately 20 tentacles, hypostome large, open and annular (preserved material).

Nematocysts, microbasic euryteles of three sizes present:

—small microbasic euryteles, capsule elliptical, $7.8 \times 3 \mu\text{m}$, shaft $5.6 \mu\text{m}$ long, spines indistinguishable, thread rather thick (Fig. 2). Abundant in tentacles.

—large microbasic euryteles, capsule bean-shaped, $21.22 \times 10.13 \mu\text{m}$, shaft $13.19 \mu\text{m}$ long, thick, armed with spines, discharges sideways, thread thick, with spirals of very fine bristles (Fig. 3). Moderately common in hypostome.

—microbasic euryteles, slightly smaller, capsule elongate, paddle-shaped, $18.19 \mu\text{m}$ long, $7 \mu\text{m}$ wide, shaft $17.18 \mu\text{m}$ long with numerous spines on distal neck region and head, thread fine (Fig. 4). Abundant around hypostome.

MEASUREMENTS, mm: *Stem*, max. proximal width, 0.075; *Branch*, maximum length, 1.1; *Pedicel*, width below hydranth, 0.075-0.1; *Hydranth*, width below tentacles (preserved material), 0.24-0.25.

REMARKS: *Eudendrium minutum* is unusual in having three different kinds of microbasic eurytele comprising the cnidome. This characteristic, and the very small size of the colonies, clearly distinguish it from all other Australian species. Kubota (1976) also described a cnidome comprising microbasic euryteles of three sizes in *E. boreale* Yamada, 1954, from Japan. This species is, however, quite distinct from *E. minutum* in both size of colony and in its heavily corrugated branches. *Eudendrium minutum* is similar in height of stem and colony characters to *E. antarcticum* Stechow, 1921, *E. tenellum* Allman, 1877, *E. insigne* Hincks, 1868 and *E. irregulare* Fraser, 1922. None of these species have been reported from the Australian region, *E. antarcticum* having been recorded from South Africa (Millard 1957, 1975, Stechow 1921, 1925) while the other three species are recorded from Japan, the Indopacific and Pacific regions (Yamada 1954, Fraser 1937). The record of *E. insigne* from New Zealand (Ralph 1953) is doubtful (pers. obs.). The cnidome of none of these species is known with certainty.

Throughout the large sample of nematocysts of *E. minutum* examined, all the spines of the largest, sideways-discharging nematocysts appeared to be solid and thorn-like. While these may be of an unusual type, it is more likely that they have failed to extend fully at discharge. The site on the hypostome of the slightly smaller, forwardly-discharging microbasic euryteles is unusual. As far as is known (Millard 1975, Bouillon pers. comm., present study), all other large hypostomal microbasic euryteles discharge sideways across the mouth, presumably in order to maximise effectiveness in capture of prey.

Eudendrium minutum is a very small and delicate species found in sheltered oceanic habitat, in very strong current flow.

ETYMOLOGY: The specific name refers to the small size of the colonies.

Eudendrium pennycuikae n. sp.

Figs 5-8

non *Eudendrium album* Nutting, 1896. Pennycuik, 1959: 167.

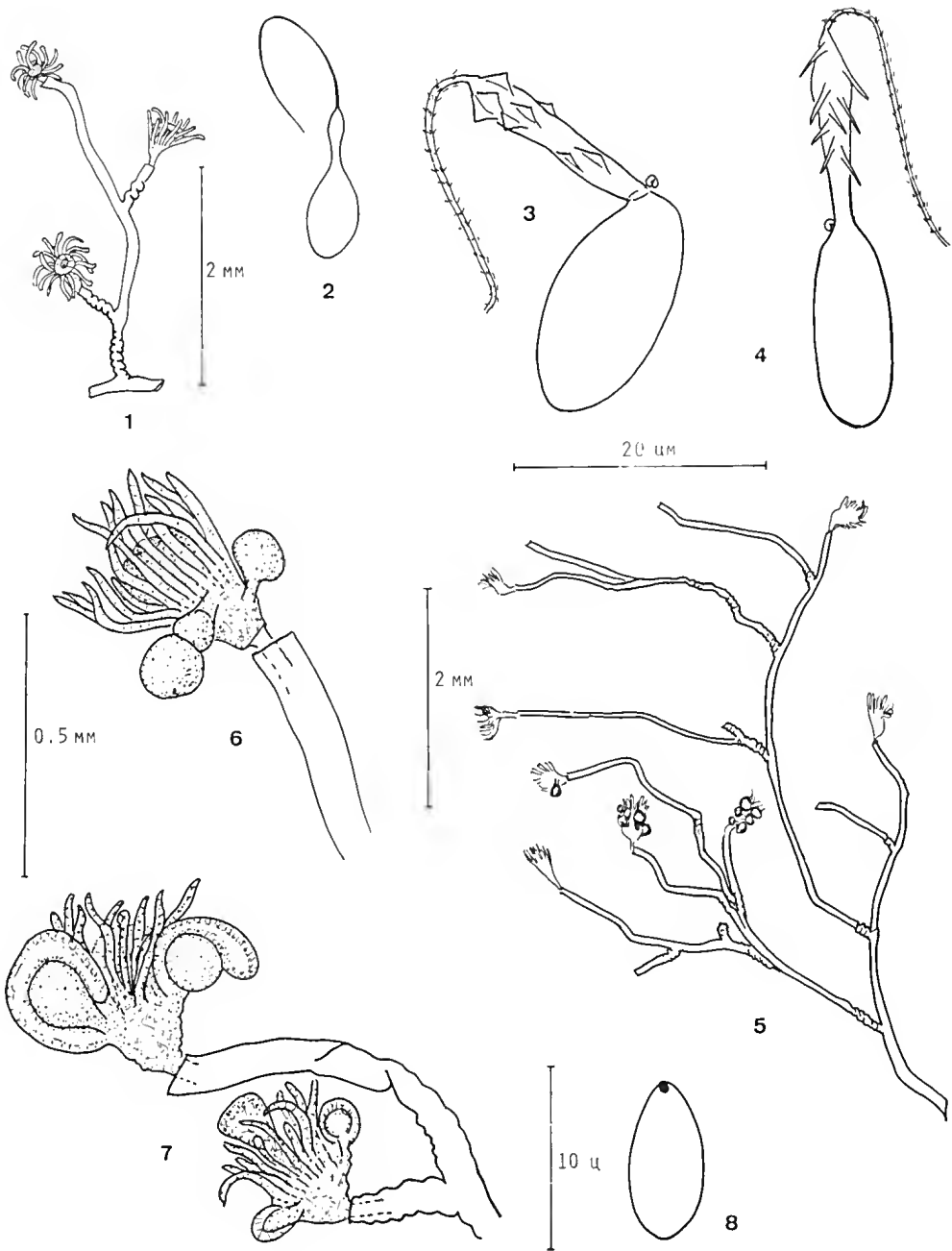
TYPE MATERIAL AND RECORD: Several colonies, alcohol preserved, on seagrass. I select as holotype a male colony, QMGL3267. Paratype: female colony, QMGL3268. All material trawled off Bundaberg, Queensland, 24° 52' S, 152° 48' E, Agassiz Trawl, 28 m, on *Halophila spinulosa* R. Brown (Aschers); coll: M. Blackburn, 14/9/1938.

DESCRIPTION FROM HOLOTYPE AND PARATYPE: Colonies comprising several stems, the largest 10 mm in height, arising from a tubular hydrorhiza wandering on the surface of the plant. Primary stems with up to 8 deep, proximal rings, no clearly-defined main stem, sparsely and irregularly branched, branches with 3-5 wrinkled annulations at origin, wrinkled or annulated at intervals throughout length. Hydranths small, slender, with a prominent hypostome (preserved material) surrounded by about 20 tentacles. Mature male gonophores bead-shaped, 2-chambered, up to 3 below a fully-developed hydranth. Female gonophores immature, with unbranched spadix, borne below a fully-developed hydranth; gonophores elongated with unbranched spadix, borne in groups of 3-5 below a fully-developed hydranth which is either shed at maturity or continues growth distally, leaving a few single gonophores scattered along the blastostyle. Nematocysts of only one kind present: small microbasic euryteles, capsule $5.8 \times 3.4 \mu\text{m}$, shaft $5 \mu\text{m}$ long, present in tentacles and body of hydranth, none discharged.

MEASUREMENTS, mm: *Stem*, max. diameter, 0.075; *Pedicel*, 0.066-0.08; *Hydranth* (preserved material), length, 0.26-0.40, diameter below tentacles, 0.17-0.27; *Female gonophore*, diameter, 0.15-0.20; *Male gonophore* diameter of distal chamber, 0.12-0.13.

COLOUR: Pennycuik (1959) gives no information on the colour of living specimens. Colour of preserved material, pale golden brown.

REMARKS: Pennycuik (1959) described, but did not figure, her specimens from Bundaberg, Queensland.



Figs 1-4—*Eudendrium minutum* n. sp. Drawn from holotype, Port Phillip Heads, Vic. 1, Whole stem. 2-4, Nematocysts, 2, Microbasic eurytele from tentacles. 3, Microbasic eurytele from hypostome, discharging sideways. 4, Microbasic eurytele from hypostome discharging in axis of capsule.

Figs 5-8—*Eudendrium pennycuikae* n. sp. 5, Whole stem, drawn from holotype, Bundaberg, Qd. 6, Hydranth with mature male gonophores, from holotype. 7, Hydranth with young female gonophores, from paratype. 8, Microbasic eurytele, undischarged, from tentacles.

Eudendrium pennycuikae compares very closely with *E. capillare* Alder, 1856 and *E. antarcticum* Stechow, 1921, especially in the possession of microbasic euryteles of only one size. I have compared Pennycuik's specimen with fertile material of *E. capillare* (BM1948.9.8.85, coll: E. T. Browne from Plymouth, U.K.) and the latter has a blastostyle with tightly-packed male gonophores and is entirely devoid of tentacles, similar to descriptions of *E. capillare* by Millard and Bouillon (1974) and Millard (1975). In contrast, the male gonophores of *E. pennycuikae* are borne on a fully-developed hydranth. Unfortunately, the paratype does not show a complete growth series of gonophores. It is likely that complete loss of the tentacles of the female blastostyle occurs near maturity.

Although the nematocysts of *E. pennycuikae* are not well preserved they are sufficiently clear to compare with a specimen of *E. album* [BM1948.9.8.83; coll: E. T. Browne, Plymouth, U.K. (no date)]. The nematocysts of this specimen, although undischarged, comprise tentacular microbasic euryteles, capsule $6.5 \times 3 \mu\text{m}$, and large bean-shaped macrobasic euryteles, $22-23 \mu\text{m} \times 9-11 \mu\text{m}$. Clearly, on the basis of this comparison, the Queensland material is not *E. album* as identified by Pennycuik (1959). Nevertheless, Bouillon (pers. comm.) considers that *E. album* has microbasic euryteles only. Such differences of opinion are indicative of the confusion surrounding the identity of even the supposedly better-known species of *Eudendrium*; it emphasises the need for critical review of the entire family.

ETYMOLOGY: This hydroid is named for Pamela Pennycuik who first recorded the species from Queensland.

Eudendrium nambuccense n. sp.

Figs 9-16

TYPE MATERIAL AND RECORDS: Holotype, MVF50508, one male colony, formalin preserved, Nambucca Heads, New South Wales, $30^{\circ} 40' \text{S}$, $153^{\circ} 0' \text{E}$, depth, 3 m on the mussel *Trichomya hirsuta* Lamarck; coll: J. E. Watson (SCUBA), 5/1/72.

OTHER MATERIAL: MVF50507, one female colony, formalin preserved, off Portsea, Victoria, $38^{\circ} 18' \text{S}$, $144^{\circ} 40' \text{E}$, depth, 12 m, on bryozoan; coll: J. E. Watson (SCUBA), 20/4/82.

DESCRIPTION OF HOLOTYPE: Colony luxuriant, comprising many stems arising from a tangled hydrorhiza on the surface of the mussel. Stems bushy, about 10 mm in height, unfascicled, irregularly and profusely branched. Perisarc of stems smooth and shining, becoming very thin and delicate distally. Primary stems ringed proximally, branches with up to 8 indistinct annulations at origin and obscurely ringed at intervals throughout their length. Hydranths small, terminal on branch, with 24-28 tentacles. A prominent ring of nematocysts ("nettle ring" of early authors) encircles the lower body of the hydranth. Male gonophores borne on lower region of colony, single-chambered, elliptical in shape when mature, each on a long stalk, in clusters of up to 15 on a cor-

rugated blastostyle. Blastostyle completely devoid of tentacles at all stages. Younger gonophores with a pronounced apical pad of nematocysts, lost at maturity. Nematocysts of only one kind present: small microbasic euryteles, capsule ranging in size from $5-9 \mu\text{m} \times 2-3.5 \mu\text{m}$, shaft $4-5 \mu\text{m}$, rather narrow with a small head armed with a few spines and a thick, ropy thread. The nematocysts fall into two fairly distinct groups within this size range, a smaller size in the tentacles and hydranth and larger ones on the gonophores.

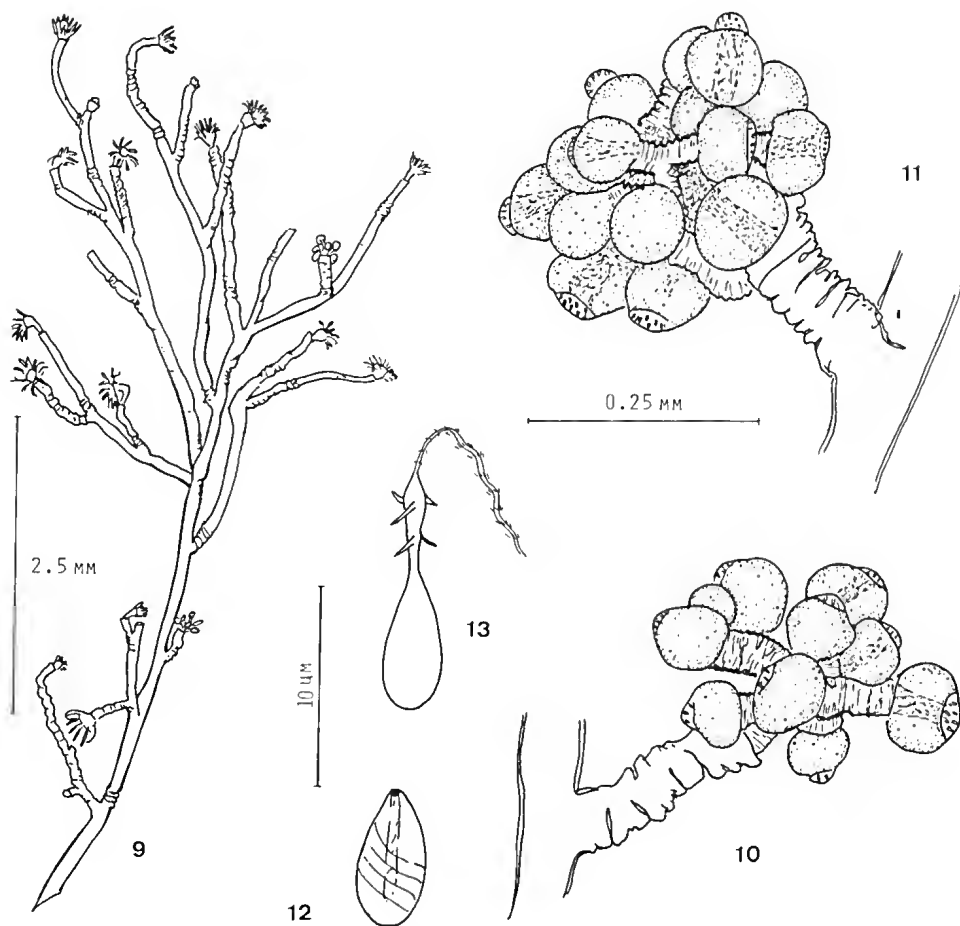
MEASUREMENTS, mm:	MVF50508 Holotype	MVF50507
Stem, maximum width	0.11	0.1
Distance between primary branches	0.3-0.8	
Width of pedicel below hydranth	0.06-0.08	0.05-0.08
Hydranth (preserved material) width below tentacles	0.1-0.18	0.15-0.24
Gonophore male, width distal chamber	0.06-0.08	
female, width mature		0.09-0.11

COLOUR: Lower stems brown, distal region creamy to colourless, colour of male not recorded.

OTHER MATERIAL: The female colony (MVF50507) from southern Australia comprises about 20 stems up to 15 mm in height. The gonophores are creamy coloured, pear-shaped, in tight clusters of 6-8 around hydranths on the lower part and mid-region of the colonies. Fertile hydranths with only half the usual number of tentacles, but these tentacles not atrophied; pedicel corrugated throughout. Spadix of female unbranched, with a conspicuous distal nematocyst pad, sometimes lost at maturity; mature gonophore enclosed in a very thick pellicle with roughened surface.

REMARKS: The nematocysts of the southern specimens overlap those of the type material in size, the smaller of the southern specimens being about the same size as the larger ones of the type. However, the length-width ratio of the capsule (Kubota 1976) remains constant at 2.5-2.6:1 over the geographic range. The larger nematocysts of both specimens are always associated with the nematocyst ring and gonophores. Since colonies of *Eudendrium* vary considerably in size and morphology with habitat and environmental conditions (pers. obs.), and the dimensions of nematocysts may also vary over the geographic range (Millard 1975, Kubota 1976, this study), the differences between the southern material and the type are not considered significant.

Eudendrium nambuccense is similar in many respects to the cosmopolitan *E. capillare* Alder, 1856, and may eventually prove to be a variant of that species. The chief differences between *E. nambuccense* and *E. capillare* as reported from the Pacific region and the southern hemisphere (Millard & Bouillon 1974, Millard 1975, Yamada 1959) are: the presence of a nematocyst ring on the hydranth and nematocyst pads on the immature gonophores of both sexes; the single-chambered male gonophore; and the reduction in number, but not



Figs 9-16—*Eudendrium nambuccense* n. sp. 9, Holotype, Nambucca Heads, N.S.W. 10, 11, Mature male gonophores with nematocyst pads. 12, 13, Nematocysts from tentacles of holotype. 12, Undischarged microbasic eurytele. 13, Microbasic eurytele, discharged. 14-16, Colony from Portsea, Vic.

size, of the tentacles of the female blastostyle of *E. nambuccense*. Although Broch (1916) reported an "accumulation of stinging cells distally" on the male gonophore of *E. capillare* from Greenland, apparently neither the female gonophores nor the hydranths of his specimens possessed aggregates of nematocysts. Mergner (pers. comm.) considers that the presence, or absence, of nematocyst pads is not necessarily specific to the identity of *E. capillare*. Several authors have described *E. capillare* as having a single kind of nematocyst ranging in length of capsule from 4-10 μm (Millard & Bouillon 1974, Millard 1975, Cooke 1975, Kubota 1976). None of these authors report a slight difference in size between the tentacular microbasic euryteles and those situated elsewhere on the hydranth and gonophores. While slight differences in size of nematocysts and presence or absence of nematocyst pads may not be individually important features at the

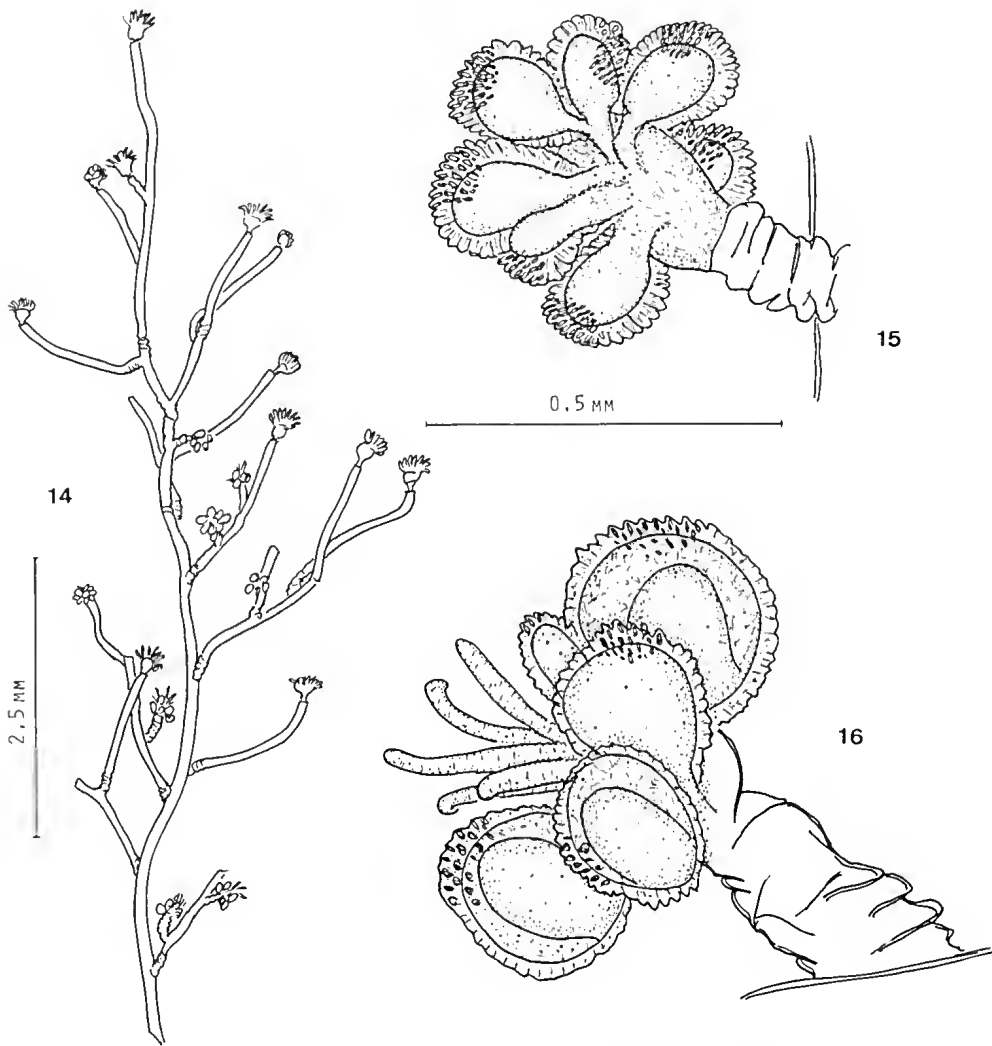
specific level, when considered together, they justify separation of the Australian material as a recognisable species, closely related to *E. capillare*.

ETYMOLOGY: The specific name refers to the type locality.

Eudendrium ?*capillare* Alder, 1856

Figs 17-19

Eudendrium capillare Alder, 1856: 355, Pl. 12, Figs. 9-12. Allman, 1864: 18; 1872: 335, Pl. 14, Figs. 1-3; 1876: 253. Van Beneden, 1866: 18, 50, 115. Hineks, 1868: 84, Pl. 14, Fig. 2. Weismann, 1883: 109, 218, Pls. 1, 2. Von Lendenfeld, 1885: 351. Thallwitz, 1885: 50. Bourne, 1890: 393. Kirkpatrick, 1890: 608. Levinsen, 1893: 154. Hartlaub, 1894: 167. Marktanner-Turneretscher, 1895: 395. Nutting, 1896: 146; 1905: 939; 1927: 201. Bonnevie, 1898: 8;



14, Stem. 15, Young female gonophore, posterior view showing nematocyst pads, tentacles obscured. 16, Female gonophore in later stages of maturity.

1899: 50; 1901: 7. Billard, 1904a: 153; 1906: 70; 1907: 338; 1912: 462. Broch, 1916: 62, Jäderholm, 1909: 11, 53, Pl. 3, Figs. 8, 9. Stechow, 1909: 29; 1913: 61, Figs. 15-17; 1919: 30, 31; 1923a: 80; 1923b: 4; 1925a: 520; 1927: 308. Vanhöffen, 1910: 290. Ritchie, 1910: 828. Fraser, 1911: 12, 24; 1912: 348, Fig. 6; 1914: 122; 1918: 18; 1937: 40; 1938: 18; 1948: 197. Kramp, 1914: 993. Balç, 1919: 335. Jarvis, 1922: 331. Lcloup, 1934: 6. Vervoort, 1941: 193; 1946: 295; 1959: 218. Vannucci, 1954: 105. Picard, 1955: 183. Yamada, 1959: 25. Naumov, 1960: 244, Fig. 132. Mammen, 1963: 57, Figs. 25, 26. Christiansen, 1972: 290. Calder, 1972: 226, Pl. 2, Fig. 6. Millard & Bouillon, 1974: 17, Figs. 3E-H. Cooke, 1975: 90, Pl. 1, Figs. 3, 4. Millard, 1975: 82, Fig. 27E-J. Rösler, 1978: 48. Hirohito, 1983: 10.

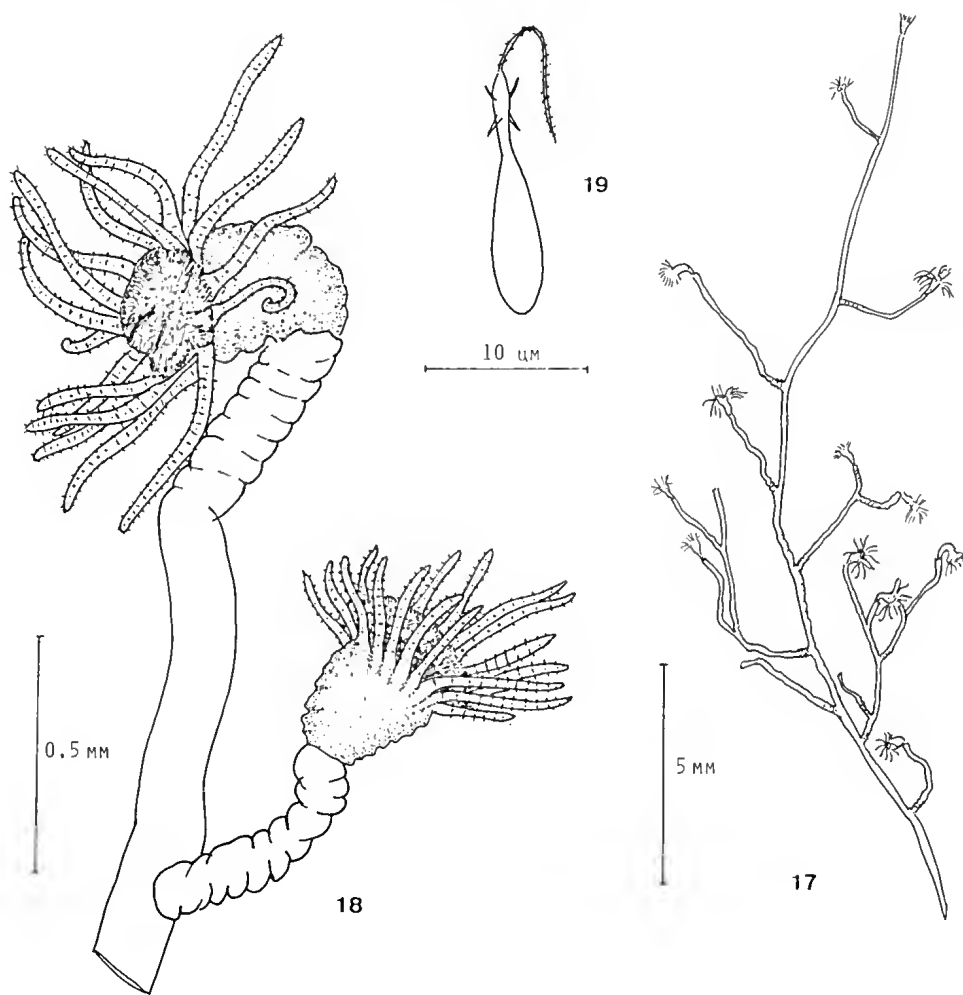
Eudendrium parvum Warren, 1908: 272, Fig. 1, Pl. 45 Figs. 1-4.

Eudendrium ?tenue Agassiz, 1865: 160.

non *Eudendrium capillare* Alder, 1856. Stechow, 1923: 69; 1925: 202. Pennycuik, 1959: 168 (in part).

MATERIAL AND RECORD: AMY242. One colony on the brown alga *Hormosira banksii* (Turner) Descainès, Port Jackson, New South Wales, 33° 52' S, 151° 25' E (no other information).

DESCRIPTION: A luxuriant sterile colony heavily investing the algal stipe. Stems up to 25 mm in height, arising from a tangled and intergrown hydrorhiza. Stems unfascicled, irregularly branched, branches bent, seldom straight, often indistinguishable from main stems. Branches with up to 10 annulations at origin, perisarc obscurely wrinkled throughout, especially on hydrothecal pedicels, but occasionally smooth. Hydranths terminal on branches, long and slender (preserved material), with a distinct proximal contraction groove but no nematocyst ring, tentacles long, filiform,



Figs 17-19—*Eudendrium capillare* Alder, 1856. Colony from Port Jackson, N.S.W. 17, Single stem. 18, Distal part of branch with hydranth. 19, Microbasic eurytele from hydranth.

nematocysts prominently displayed, hypostome wide, annular. Nematocysts of one size only, microbasic euryteles, $7-8 \times 2.5-3.5 \mu\text{m}$, shaft $6 \mu\text{m}$, slender, with a few short spines, thread very long and ropy. Moderately abundant on tentacles, absent from hypostome.

MEASUREMENTS, mm: *Branch*, maximum length, 6.7, width at origin, 0.15-0.18, width below hydranth, 0.1-0.13; *Hydranth* (preserved material), width below tentacles, 0.2-0.25, length of body, 0.25-0.45.

REMARKS: As the specimens show characters differing from *E. nambuccense* such as a long, slender hydranth, absence of a nematocyst ring, more annulated branches and pedicels, and number of tentacles, they are here tentatively assigned to *E. capillare*. The main basis of referral is the resemblance to the description of *E. capillare* by Millard (1975). Confirmation of this diagnosis must await the finding of fertile Australian material. The presence of a nematocyst ring on the hydranth would,

however, confirm the species as *E. nambuccense*, not *E. capillare*.

No information is available about the specimen other than the locality, and a note that it was purchased from T. Whitelegge. This indicates that the specimen has probably been in the Australian Museum collection since late last century. Stechow (1923, 1925a) recorded *E. capillare* from Freycinet Reach, Western Australia. Later, Pennycuik (1959) reported the species from Queensland. Examination of Stechow's specimens, loaned by the Naturhistorisches Museum of Vienna, shows that this material is not *E. capillare*; rather, it is identical with a hydroid reported as *E. generale* by Kirkpatrick (1890) from Torres Strait. This hydroid is described elsewhere (p. 194) as a new species. Pennycuik (1959, p. 168) recorded *E. capillare* from Currumbin in southern Queensland and from the Low Isles on the northern Great Barrier Reef. I have examined Pennycuik's

specimens and find that although the meagre Low Isles material is sterile, the abundant undischarged microbasie euryteles suggest that it may be *E. capillare*. Conversely, the presence of heteronemes in the Currumbin specimen clearly demonstrates that this is not *E. capillare*. The latter material is also described in this paper as a new species (p. 209).

Eudendrium terranovac n. sp.

Figs 20-23

?*Eudendrium novaezelandiae* Marktanner-Turneretscher, 1890. Totton, 1930: 141. Farquhar, 1895: 209; 1896: 459. Rösler, 1978: 112, Pl. 20, Fig. 6.

Abundant material of a hydroid found in Bass Strait, Victoria, led to comparison of this material with the specimen taken at North Cape, New Zealand, by the "Terra Nova" expedition and assigned, with considerable doubt by Totton (1930), to *E. novaezelandiae* Marktanner-Turneretscher, 1890. Of *E. novaezelandiae*, Totton remarked that it was "difficult to extract from the original description any diagnostic specific characters". I have examined Totton's specimen and compared it with the type of *E. novaezelandiae*. Examination, especially of the nematocysts, demonstrates conclusively that Totton's specimen is not *E. novaezelandiae*: it is here considered to be a new species, described below. The holotype of *E. novaezelandiae*, and material recently collected in New Zealand, will be described elsewhere (Watson, in prep.).

TYPE MATERIAL AND RECORD: Holotype, one sterile colony, alcohol preserved, BM1929.10.28.11, "Terra Nova" Expedition 1910-1913, Stn 134, North Cape, New Zealand, 34° 18' S, 172° 20' E, depth, 20-37 m, bottom shelly, dredge.

DESCRIPTION OF HOLOTYPE: Colony 50 mm high, dichotomously branched halfway up stem. Stem strongly fasciated to about two-thirds height of colony, branches passing outwards at about 30°, in one plane, with up to 5 proximal annulations, a few superficial annulations at intervals along length, perisarc otherwise smooth and shining. Hydrothecal pedicels rather long, alternate, mostly in one plane at either side of branch, a few directed anteriorly, most curved, but some straight, with 1-4 indefinite proximal annulations, otherwise smooth or indistinctly ringed at intervals. Hydranths well preserved, of moderate size, body long, with a clavate to trumpet-shaped hypostome and 24-28 tentacles, a deep proximal groove around body but no nematocyst ring. Nematocysts abundant, of one kind only: microbasie euryteles, undischarged, capsule pyriform, 6-7 $\mu\text{m} \times 2-3 \mu\text{m}$, in tentacles and on body of hydranth.

MEASUREMENTS, mm: *Stem*, proximal width, 1.24, distance between alternate branches, 0.9-1.08; *Branch*, length, 2.3-10.8, width at origin, 0.15-0.16; *Hydranth* (preserved material), length of pedicel, 0.7-1.54, width at origin, 0.13-0.18; distance between pedicels, 1.8-2.0, width of body below tentacles, 0.25-0.3.

OTHER MATERIAL: BM1983.8.9.2, one male colony;

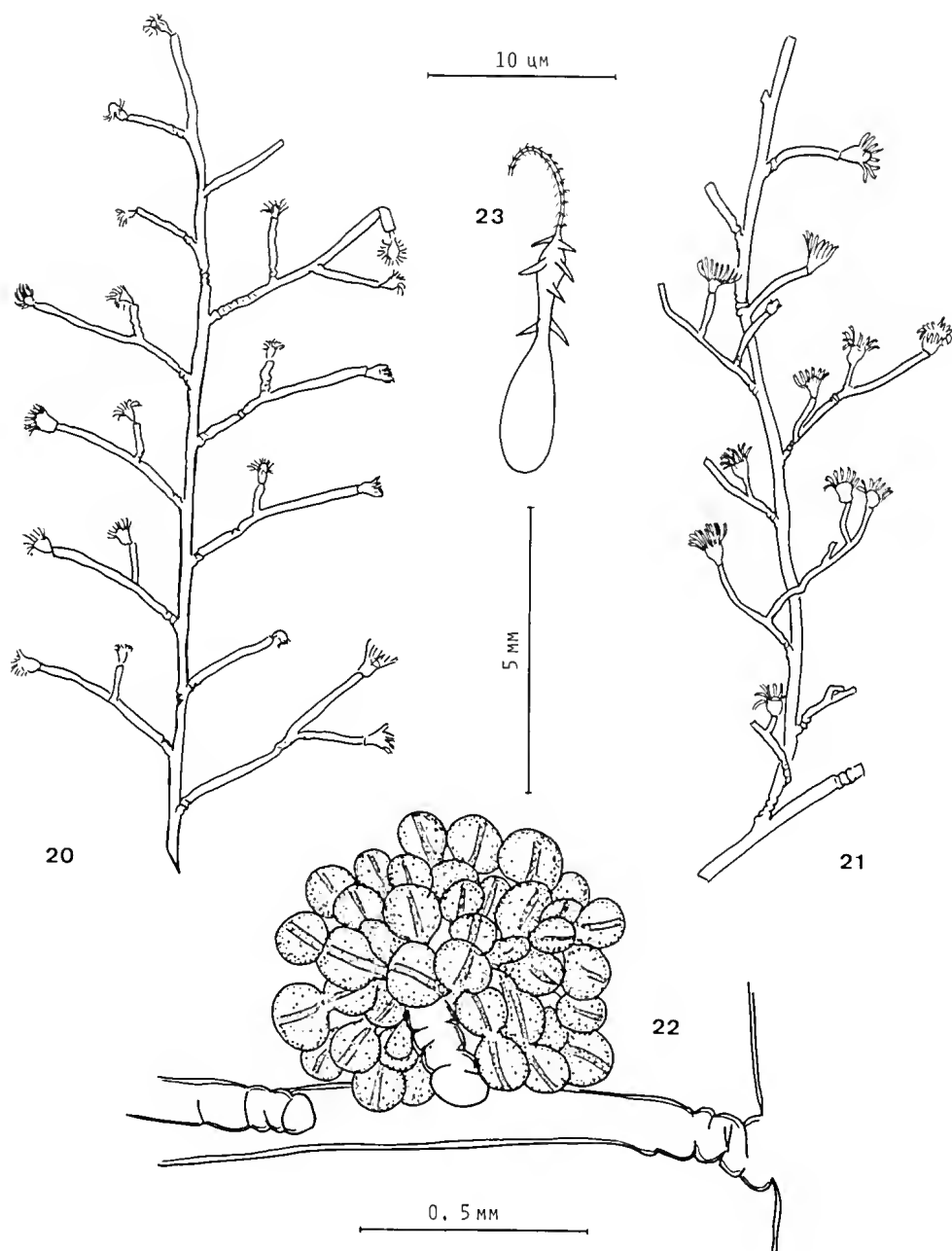
MVF50503, male colony; MVF50504, female colony; all material alcohol preserved; Clifly Island, Bass Strait, 38° 56' S, 146° 43' E, from small caverns and under ledges, depth 10 m; coll: J. E. Watson (SCUBA) 20/5/83. MVF50505, alcohol preserved, Clifly Island, Bass Strait, under ledges, depth 15 m; coll: J. E. Watson (SCUBA) 19/8/82. Additional material also held in collection of author.

SUPPLEMENTARY DESCRIPTION: Colonies up to 6 cm high, the largest comprising 6 stems growing from a common rootstock; other colonies consisting of single stems. Stems erect, straight or sometimes gnarled and bent in proximal region, heavily fasciated for about two-thirds height, fascicular tubes also running along older branches. Branching regularly alternate, mostly in one plane, some rebranching in older, lower parts of stem, branches with up to 9 proximal annulations. Hydranth pedicels alternate on branch, usually in same plane, sometimes anteriorly directed, variable in length, straight or curved, smooth or indistinctly annulated throughout entire length. Body of living hydranth elongate, very extensile with a prominent hypostome and 28-30 long tentacles.

Nematocysts, small microbasie euryteles, capsule 5-6 $\mu\text{m} \times 2 \mu\text{m}$, shaft 5-6 μm , distally inflated, with a few distal spines and a relatively long thread. Moderately abundant in tentacles, a few around hypostome and some scattered on the male gonophores. Gonophores borne on separate colonies, both sexes most numerous on branches in upper third of colony, but absent from distal region of branch. Male gonophores small, 2-chambered, in tightly-packed clusters of about 30 in all phases of development on a blastostyle completely devoid of tentacles at all stages. Distal chamber of immature gonophore peaked, mature gonophore globular. Female gonophores immature, a few borne on a blastostyle showing atrophy of the tentacles from early growth stages, tentacles completely absent at maturity. MEASUREMENTS, mm: *Stem*, max. proximal width, 1.85; distance between branches, 1.2-1.4; *Branch*, max. length, 32, width at origin, 0.18-0.25; *Hydranth* (preserved material), length of pedicel, 0.2-1.2, width at origin, 0.13-0.15, distance between pedicels, 0.9-1.34, width of body below tentacles, 0.35-0.45 (living material) max. length of body, 0.3; max. width below tentacles, 0.18-0.43; width across extended tentacles, 2.25; height of hypostome (clavate), 0.15; width across hypostome (annular), 0.38.

COLOUR: Older stems of living material dark brown, grading to lighter brown on younger parts. Body of hydranth variable in colour, from creamy to light brown, hypostome and tentacles white. Mature male gonophores clear, spadix flesh pink.

REMARKS: The Australian specimens are larger and more robust and show a tendency towards less orderly branching than the holotype. The microbasie euryteles are also slightly larger, but the length-width ratio of the capsule is similar (2.5-3:1). *Eudendrium terranovae* is very close to *E. deciduum* Millard, 1957 in size of colony and in possessing only one kind of nematocyst. The abun-



Figs 20-23 — *Eudendrium terranova* n. sp. 20, Branch from holotype, North Cape, New Zealand ("Terra Nova" Expedition). 21, Branch of colony from Clifty Is., Bass Strait, Vic. drawn to same scale. 22, Mature male gonophores from Clifty Is. specimen. 23, Microbasic eurytele from Clifty Is. specimen.

dant Bass Strait material shows that the planar habit of *E. terranova* is a consistent feature, characteristic of the species, which differentiates it from the more irregularly branched *E. deciduum*. *Eudendrium terranova* also resembles *E. armatum* Jäderholm, 1909, in colony morphology and possession of only one kind of nematocyst (Bouillon pers. comm.). However, *E. armatum* (known to me only from the literature) has a deeply corrugated hydrothecal pedicel (Jäderholm 1909), a feature not present in *E. terranova*.

This taxon is the only trans-Tasman species of *Eudendrium* so far recorded. It is a common oceanic hydroid at Cliffy Island, offshore from Wilsons Promontory in eastern Bass Strait. It occurs from early to late winter in the sheltered habitat of small caverns at depths of 10-25 m. Several colonies, evidently young ones, which were collected at Cliffy Island from a green alga, *Caulerpa flexilis* Lamouroux, were stolonial and unfascicled. At this stage they closely resemble, and are difficult to distinguish from *E. capillare* Alder, 1856.

LABORATORY OBSERVATIONS: Observation on living specimens of *E. terranova* revealed that the conspicuously-extended clavate hypostome and outstretched tentacles is the normal resting position of the hydranth. When irritated by a probe, the tentacles close and the hypostome instantly retracts to the wide annular or trumpet-shaped hypostome often considered to be a diagnostic feature of *Eudendrium*. Resumption of the resting position occurred within 12-25 sec, measured over 10 hydranths. Four to five consecutive responses could be elicited at increasing time intervals before the hydranth completely failed to respond. This behaviour suggests that, in contrast to species with a more complex cnidome, *E. terranova* may compensate for its limited nematocyst armament by possession of a very reactive hypostome. In this way, more reliance is placed upon rapid engulfment by the hypostome rather than on entanglement of prey by tentacular threads.

ETYMOLOGY: The species is named after the "Terra Nova", the vessel of the British Antarctic Expedition, 1910.

Eudendrium corrugatum n. sp.

Figs 24-28

TYPE MATERIAL AND RECORD: Holotype MVF50506, one female colony, formalin preserved. Northern Stradbroke Island, 27° 20' S, 153° 35' E, on reef, depth 33 m; coll: R. Willan (SCUBA), 17/6/81.

DESCRIPTION OF HOLOTYPE: Colony comprising three stems 10 cm, 4 cm and 2.5 cm in height, arising from a common rootstock. Main stems strongly fascicled, smooth and shining, the fascicular tubes running from the hydrorhizal filaments to about halfway up the stem and sometimes for a short distance along the branches. Stems alternately branched in one plane in a regular manner, the longest branches in the mid-stem region, upwardly directed (in longest stem) or extending straight out in the smaller stems, occasionally with secondary rebranching. Branches with 8-10 deep annulations at

origin, main stem also ringed at intervals, usually below origin of a branch. Hydrothecal pedicels short, regularly alternate, most given off in plane of branch, short, chiefly straight or sometimes slightly curved, deeply ringed over most or all of their length. Only reproductive hydranths present. Female gonophores borne on lower half of colony, the blastostyle given off as a short secondary pedicel from pedicel of hydranth, 4-6 gonophores present in a cluster below hydranth. Reproductive hydranth without hypostome but with approximately 30 tentacles which may be either atrophied or completely absent. Immature gonophore enclosed in an unbranched spadix, lost at maturity, mature gonophore globular, comprising a single egg enclosed in a thin pellicle; one to five gonophores clustered on blastostyle at late maturity. Nematocysts, small microbasic euryteles of one size only, capsule 8-9 μ m long \times 4 μ m wide, none discharged, a few scattered in tentacles of the blastostyle; a few also on the gonophores.

MEASUREMENTS, mm: *Stem*, proximal width, 1.5, width of fascicular tube of stem, 0.18-0.2; *Branch*, width at origin, 0.23-0.25, maximum length, 40.0, distance between branches, 1.5-3.0; *Hydranth* pedicel, length, 0.5-1.6, width, 0.15-0.2; *Gonophore*, width of mature female, 0.25-0.33.

COLOUR: Main stem deep shining brown, other stems lighter brown.

REMARKS: This large species is characterised by its conspicuously planar form and orderly, alternate branching. Although the only hydranths remaining on the colony are those bearing gonophores, the tentacles of these provide a reasonable estimate of the number on the sterile hydranth. The nematocysts are unusually small and sparse, particularly on the tentacles of the hydranth. *Eudendrium corrugatum* is similar to *E. deciduum* Millard, 1975 from South Africa, and *E. cyathiferum* Jäderholm, 1904 from South Georgia. It differs from the former species in having an unbranched spadix of the female gonophore and differs from the latter species in the more strongly annulated pedicel of the hydrothecal pedicel and blastostyle, as, according to Jäderholm's (1904) figure, the blastostyle of *E. cyathiferum* is not annulated. In some respects, *E. corrugatum* also resembles *E. rameum* Pallas, 1766, in the large size of the colony and in having only one kind of nematocyst (Bouillon pers. comm.). However, since descriptions of *E. rameum* (Allman 1872, Hincks 1868) stress the irregular and profuse branching and strong fasciculation of that species, the Australian specimen is here considered to be a separate species.

ETYMOLOGY: The specific name refers to the neatly corrugated pedicels.

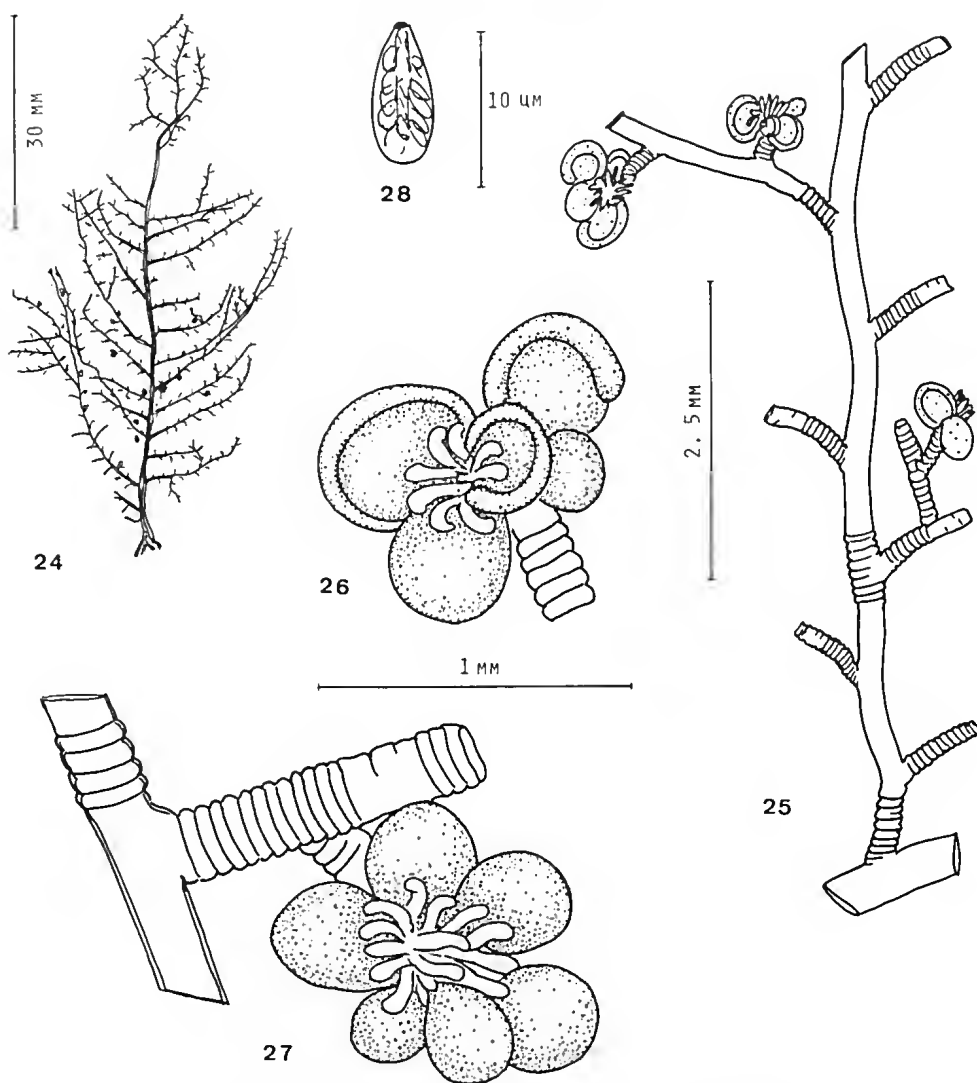
Eudendrium ramosum (Linnaeus, 1758)

Figs 29-34

Corallina tubularia gracilis Ellis, 1755: 31, Pl. 16, Fig. a, Pl. 17, Fig. A,a.

Tubularia ramosa Linnaeus, 1758: 804; 1761: 539.

Tubularia trichoides Pallas, 1766: 84.



Figs 24-28—*Eudendrium corrugatum* n. sp. Drawn from holotype, Stradbroke Is., Qd. 24, Whole colony. 25, Part of branch with female gonophores. 26, 27, Female gonophores. 26, young and mature gonophores. 27, mature gonophores on blastostyle with partly-atrophied tentacles. 28, Microbasic eurytele from hydranth, undischarged.

Tubularia ramosa Linnaeus, 1767: 1302.

Tubularia trichoides Pallas, 1787: 120.

Tubularia ramosa Lamouroux, 1812: 185. Lamarek, 1816: 110.

Tubularia trichoides Lamouroux, 1816: 231.

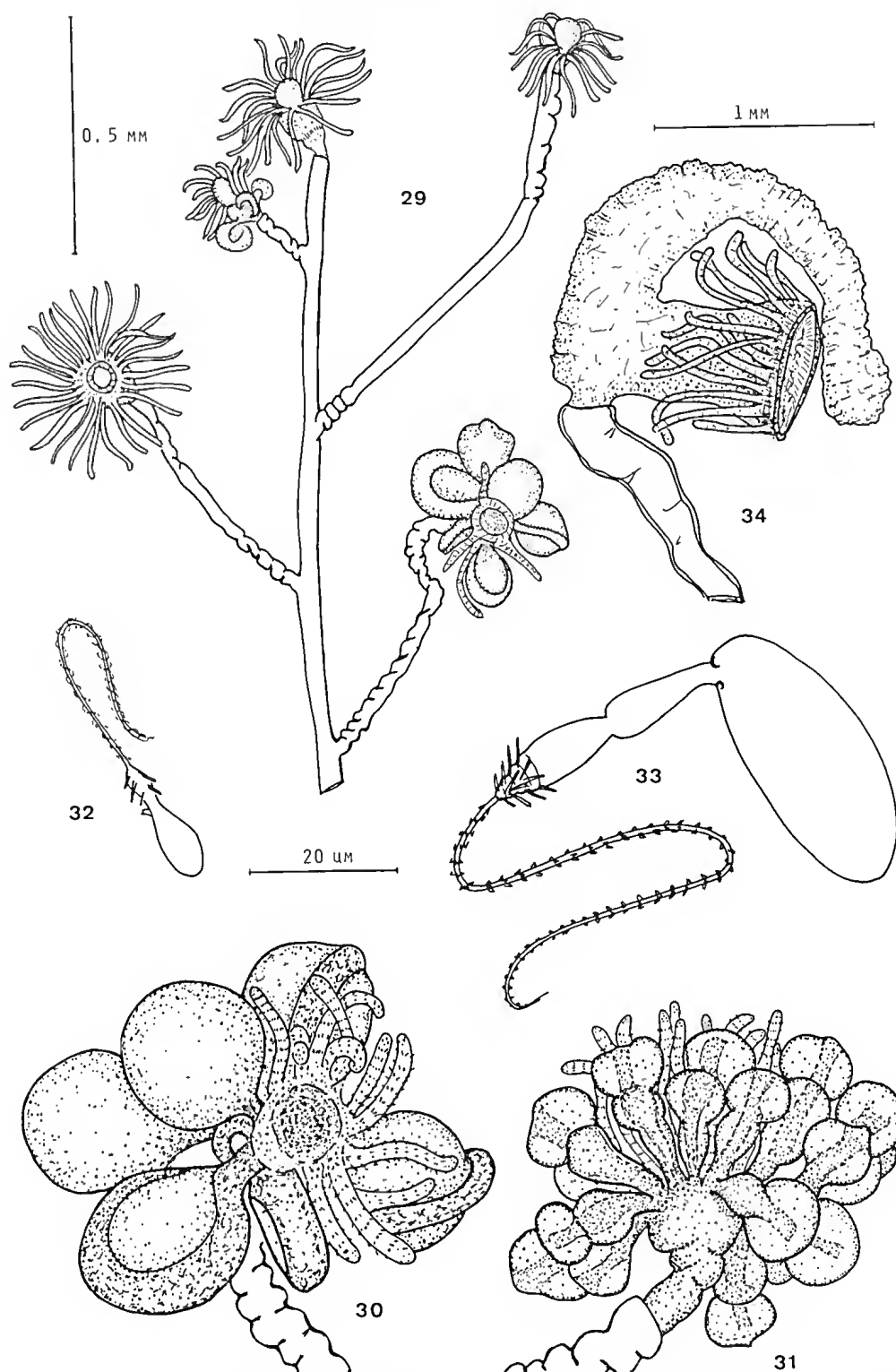
Tubularia ramosa Lamouroux, 1821: 17.

Eudendrium ramosum Ehrenberg, 1834: 296. Thompson, 1844: 283. Gray, 1848: 63. Sars, 1851: 131, 136. Alder, 1858: 103. Wright, 1858: 448. L. Agassiz, 1860-62: 342. Hineks, 1861: 159; 1868: 82, Pl. 13. Allman, 1864a: 362; 1871: 332, Pl. 13, Figs. 1-17. A. Agassiz, 1865: 224. Weismann, 1880: 227. Marktanner-Turneretscher, 1890: 201. Fraser, 1912: 349, Fig. 8; 1944: 72, Pl. 12, Fig. 48. Broch, 1916: 59. Stechow, 1923a: 83. Vervoort, 1946a: 147, Figs. 58, 59. Picard, 1955: 183. Riedl, 1959: 623. Millard,

1966: 456; 1975: 85, Fig. 31. Millard & Bouillon, 1973: 32, Fig. 4; 1974: 19, Fig. 3. Wedler, 1970. Mergner & Wedler, 1977: 12, Pl. 1, Fig. 5. Mergner, 1977: 119-125. Rösler, 1978: 127, Pl. 24, Figs. 1-7.

MATERIAL AND RECORDS: MVF50509, female colony, formalin preserved; coll: J. E. Watson, 20/4/82. MVF50721, male colony, part formalin, part alcohol preserved; coll: J. E. Watson (SCUBA) 20/4/82. All material from side of deep water channel, depth 25 m, Port Phillip Heads, Victoria, 38° 18' S, 144° 40' E. MVF 50511, Bagara reef, Hervey Bay, Queensland, 24° 50' S, 152° 20' E, depth, 6 m; coll: J. E. Watson (SCUBA), 11/11/75.

DESCRIPTION: Colonies up to 20 mm in height. Hydorrhiza tubular, wandering over and through the substrate, becoming erect at intervals as single



Figs 29-34—*Eudendrium ramosum* (Linnaeus, 1758). 29, Distal part of stem from colony, Port Phillip Heads, Vic. 30, Immature and mature female gonophores. 31, Mature male gonophores. 32, 33, Nematocysts. 32, Microbasic eurytele from tentacles. 33, Large microbasic eurytele from hypostome. 34, Aberrant hydranth with pseudo-cnidophore from colony from Hervey Bay, Qd.

stems. Stems thick and smooth, unfasciated, sparingly and irregularly branched with up to 10 branches, rebranching common. Stems with 6-12 distinct proximal annulations, ringed at intervals throughout length, branches with 6-10 annulations just above origin. Hydranths terminal on branches, pedicels indistinctly annulated at intervals, widening distally, sometimes terminating obliquely below hydranth. Hydranths large, with 24-30 tentacles (very long in life), a distinct proximal groove in the lower body of some, but not all hydranths. Hypostome large, annular to clavate in preserved material.

Sexes on separate colonies, the gonophores scattered on all but the most distal branches. Male gonophores in all stages of maturity borne in a single crowded verticil below a hydranth with a fully-developed hypostome and a full number of partially-atrophied tentacles. Mature gonophore 3 or 4-chambered, immature gonophore with a rod-shaped spadix and a small apical knob without nematocyst pad. Mature gonophore globular or bun-shaped, apical tubercle lost at this stage. Female gonophores borne low on stem, clustered in all stages of development below a hydranth with hypostome and a full number of partially-atrophied tentacles. Young gonophores on a long, thin pedicel, disk-shaped with unbranched spadix, mature gonophores retained below hydranth, oval, containing a single egg encased in a tough gelatinous pellicle.

Nematocysts, microbasic euryteles of two sizes present:

- small microbasic euryteles, capsule $8-9 \times 3-4 \mu\text{m}$, shaft $6-8 \mu\text{m}$ long, with very long thread. Abundant in tentacles (Fig. 32).
- large microbasic euryteles, capsule $38-43 \times 15-18 \mu\text{m}$, bean-shaped, shaft discharging sideways, $30-36 \mu\text{m}$ long, distal end inflated and spirally annulated, with numerous bristles arising from the annulations, thread very long with distinct spines (Fig. 33). Abundant around hypostome and scattered in groups over spadix of immature female gonophore.

MEASUREMENTS, mm: *Hydrorhiza*, stem and branches, width, 0.2-0.25; *Branch*, maximum length, 6.0; *Hydranth* (living material), width below tentacles, 0.4-0.5, max. width across extended tentacles, 2.0; *Hydranth* (preserved material), max. width below tentacles, 0.5; *Pedicel*, width distally, 0.2-0.25, width proximally, 0.13-0.15; *Gonophore*, width of mature female, 0.65-0.75, max. length of mature male series, 0.63, max. width distal chamber, 0.3.

COLOUR: Stems golden brown, body of living hydranth yellow or orange pink, tentacles pale yellow to pink, spadix of female gonophore purplish pink, mature eggs orange, male gonophores pearly pink, spadix orange pink.

REMARKS: None of the material of *E. ramosum* shows any tendency towards the tall, basally-fasciated colonies considered typical of the species by Millard & Bouillon (1973, 1974). The colonies more closely resemble the smaller colonies reported on weed and other hydroids by

Millard (1975). Mergner (pers. comm.) considers that the larger, arborescent colonies of *E. ramosum* are usually found in deeper, calm waters and that smaller colonies, like the present material, are usually associated with stronger water movement. The occurrence of *E. ramosum* in the swift-flowing tide channel at Port Phillip Heads, Victoria, is in accordance with Mergner's view.

The tightly clustered male gonophores of the Australian specimens are in contrast to the sparse whorl of 4-8 gonophores reported by Rösler (1978) in *E. ramosum* from the Mediterranean Sea. Although the supplementary microbasic euryteles of the Australian specimens are 30-50% larger than those reported by Millard (1975) for her South African material, the length-width ratio is similar (Australian, 2.4-2.5:1; South African 2.1-2.5:1). Despite this discrepancy in size, the spirally-armed, sideways-discharging nematocysts are sufficiently distinctive to enable provisional assignment of the Australian material to *E. ramosum*.

About 20% of the hydranths of the Queensland specimens show peculiar outgrowths from the lower body, resembling cnidophores. Detailed examination revealed these to be hollow structures connected to the body cavity of the hydranth. Although nematocysts occur on these structures they are aggregated on the proximal, not the distal end as in true cnidophores. Examination of thin sections of these "pseudocnidophores" showed no evidence of parasitic encystment or of foreign larvae. The origin and significance of these structures, occurring only in the tropical material, is therefore unknown.

Eudendrium ramosum is known from Britain, the North Atlantic from the Arctic to the Cape Verdes, the Mediterranean Sea, the Seychelles, South Africa (Millard 1975), the West Indies and the Red Sea (Mergner 1972, 1977). This species is a very common and conspicuous hydroid in the community of the tidal channel at Port Phillip Heads and in other oceanic localities in central Bass Strait where there is good water movement. The distinctively yellow, straggling, but robust colonies occur throughout most of the year, creeping on bryozoans (especially *Sertella granulata* MacGillivray), compound ascidians, sponges and occasionally on red algae. The species is fertile over the winter months.

Eudendrium kirkpatricki n. sp.

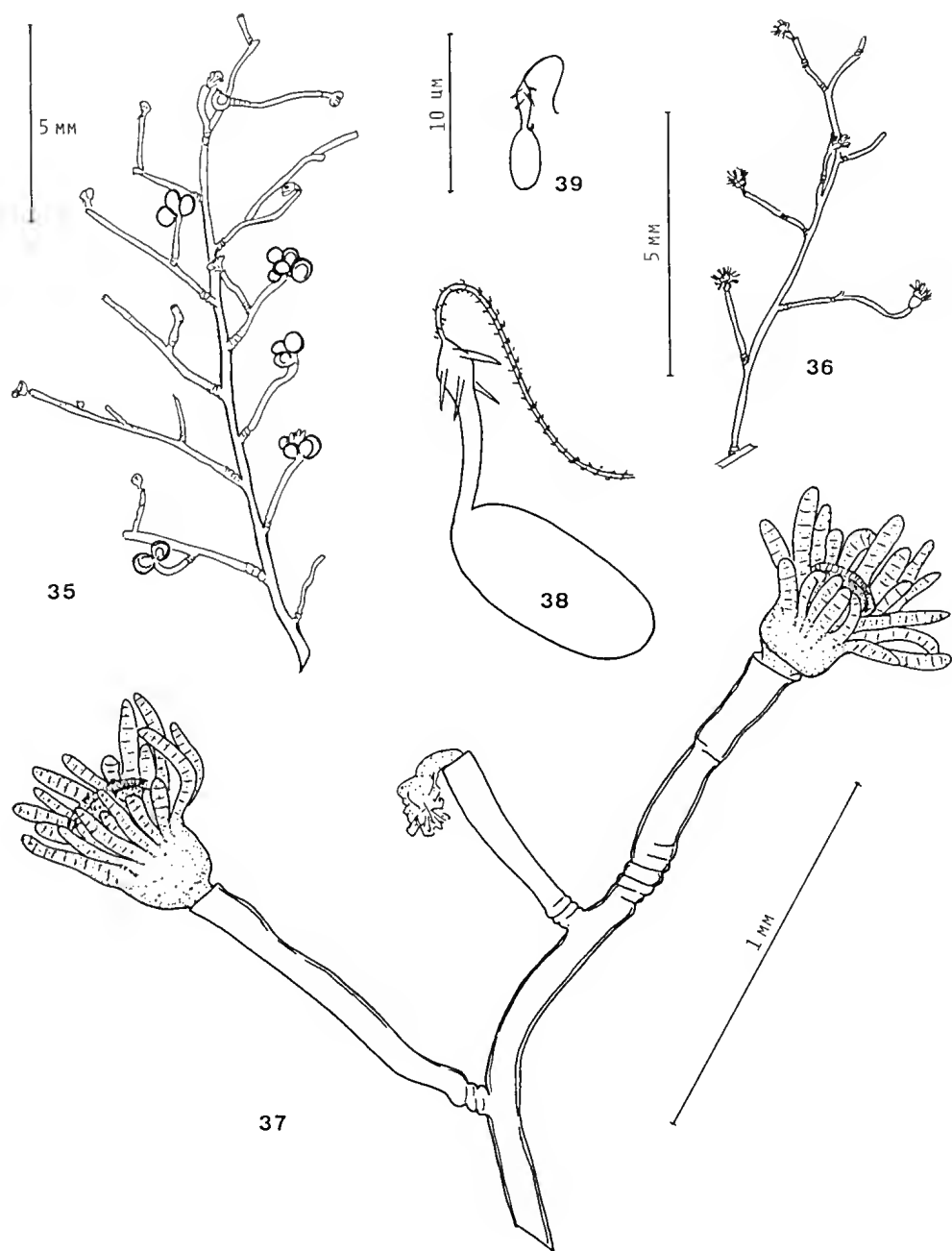
Figs 35-39

Eudendrium generalis von Lendenfeld, 1885.

Kirkpatrick, 1890: 607, Pl. 15, Figs. 1, 2.

Eudendrium capillare Alder, 1856. Stechow, 1925a: 202.

Kirkpatrick (1890) assigned material from Warrior (Tud) Is. and Murray Is. in Torres Strait to *E. generale* von Lendenfeld, 1885. I have examined Kirkpatrick's material and compared it with the type of *E. generale*. Kirkpatrick's specimen is not *E. generale*, but an undescribed species.



Figs 35-39—*Eudendrium kirkpatricki* n. sp. 35, Part of stem, from microslide, BM1890.3.24.113, part of holotype from Torres Strait. 36, 37, Specimen from Port Moresby, Papua New Guinea. 36, Whole stem. 37, Distal part of stem. 38, 39, Nematocysts, drawn to same scale. 38, Microbasic eurytele from hypostome of specimen from Hervey Bay, Qd. 39, Small microbasic eurytele from tentacles of specimen from Papua New Guinea.

TYPE MATERIAL: 1 select as holotype, BM1890.3.24.113-120, female colony, alcohol preserved (and also microslide preparation, BM1890.3.24.113 from same colony), Murray Is., 9° 55' S, 144° 8' E, depth 27-37 m.

OTHER MATERIAL: BM1890.11.22.35, microslide, part of male colony, Warrior (Tud) Is. 9° 30' S, 142° 54' E, Stn 2; BM1890.11.23.33, male and female stems, alcohol preserved, Warrior Is. MVF50512, Port Moresby, Papua New Guinea, 9° 30' S, 147° 10' E; colony formalin preserved, on worm tube from coral reef, 2-3 m deep; coll: J. E. Watson, June 1981. MVF50513, Hervey Bay, Queensland, 24° 50' S, 152° 20' E; colony formalin preserved, on barnacles from reef, depth, 6 m; coll: J. E. Watson (SCUBA), 14/11/75.

DESCRIPTION: The following description from the holotype and other material supplements that of Kirkpatrick (1890). The Murray Is. (holotype) specimens comprise a colony of about 30 stems up to 20 mm in height, on *Sciurella indivisa* (see Kirkpatrick 1890, p. 608). The Warrior Is. specimens comprise several broken stems, the tallest of which is 43 mm high. Stems unfascicled, main stem straight, perisarc smooth, shining, obscurely annulated at intervals. Branches irregularly alternate, more or less in one plane, upwardly directed, some secondary branching present; branches with a few proximal annulations, widening a little distally. Hydranths small, but too poorly preserved for a tentacle count. Female gonophores borne on all except distal parts of colony, 3-6 in various stages of development tightly clustered around a hydranth, spadix of immature gonophore unbranched. Mature blastostyle devoid of tentacles, the egg-shaped gonophores remaining clustered in their original positions on blastostyle. Male gonophores borne in a verticil below a fully-developed hydranth, 2-chambered and bead-shaped at maturity.

Nematocysts, microbasic euryteles of two sizes present, few discharged:

- small microbasic euryteles, capsule $7 \times 3-4 \mu\text{m}$, very abundant in tentacles (Fig. 39).
- larger microbasic euryteles, capsule bean-shaped, $29-30 \times 13-15 \mu\text{m}$, shaft (seen through wall of capsule), approximately $22 \mu\text{m}$ long, with a very long, coiled thread. Moderately abundant around hypostome (Fig. 38).

MEASUREMENTS, mm: *Stem*, width, 0.18-0.2; *Branch*, maximum length, 0.5-2.75; distance between branches, 0.7-1.8; *Hydranth*, pedicel, proximal width 0.1-0.13, distal width, 0.13-0.18; *Gonophore*, male, length at maturity, 0.23-0.3, width of distal chamber, 0.13-0.15, female, length, 0.28-0.35.

COLOR: The colonies were probably cream-coloured or yellow in life and the male gonophores deep pink or red.

REMARKS: It is virtually impossible to distinguish between some of the smaller, shrubby species of *Eudendrium* using colony characteristics alone, even when gonophores are present. For example, *E. generale*, *E. capillare* and other small Australian species which are very similar in colony morphology can only be satisfactorily distinguished from each other and from *E. kirkpatricki* by examination of the endome. Even if the nematocysts are undischarged, *E. kirkpatricki* can be readily separated from the foregoing species by this means. Although the nematocysts are undischarged in the type material, fully-discharged nematocysts are present in the material from Port Moresby, Papua New Guinea, and from Hervey Bay, Queensland. The smaller, tentacular nematocysts have a rather short, inflated shaft with a few spines. The larger microbasic euryteles always discharge sideways, have a long slender shaft and an small head armed with a few thorn-like spines. The thread bears distinct spirals of bristles.

Through courtesy of the Zoologisches Museum, Hamburg I have been able to examine specimens from Freyeinet Reach in Western Australia referred, by Stechow (1923, 1925a), to *E. capillare* Alder, 1856. The endome of Stechow's material comprises microbasic euryteles of two distinct sizes, which immediately distinguishes the species from *E. capillare*, a species with microbasic euryteles of only one size or slightly-differing sizes. The longer microbasic euryteles of Stechow's specimens are slightly smaller, but otherwise identical to those of the holotype of *E. kirkpatricki*. Since nematocysts may show some variation in size over their geographic range, the difference between the endome of the two species is not here considered significant. Stechow's material is therefore assigned to *E. kirkpatricki*.

DISTRIBUTION: *Eudendrium kirkpatricki* is one of the most widely distributed of all Australian species of *Eudendrium*, ranging from the southern Great Barrier Reef on the Pacific coast, north to Papua New Guinea and to the western, Indian Ocean, side of the continent. ETYMOLOGY: The species is named after R. Kirkpatrick who first recorded it from Torres Strait.

Eudendrium generale von Lendenfeld, 1885

Figs 40-52

Eudendrium generale von Lendenfeld, 1885: 351, Pl. 6; 1885a: 621; 1887: 16.

Eudendrium generale von Lendenfeld, 1885a: 621. Hartlaub, 1905: 515. Stechow, 1921: 416.

?*Eudendrium generale* von Lendenfeld, 1885. Jarvis, 1922: 333.

non *Eudendrium generale* von Lendenfeld, 1885. Kirkpatrick, 1890: 607, Pl. 15, Figs. 1, 2. Ritchie, 1910: 805.

non *Eudendrium generale* von Lendenfeld. Bale, 1919: 335. Watson, 1982: 89, Fig. 4.6j, Pl. 10.3.

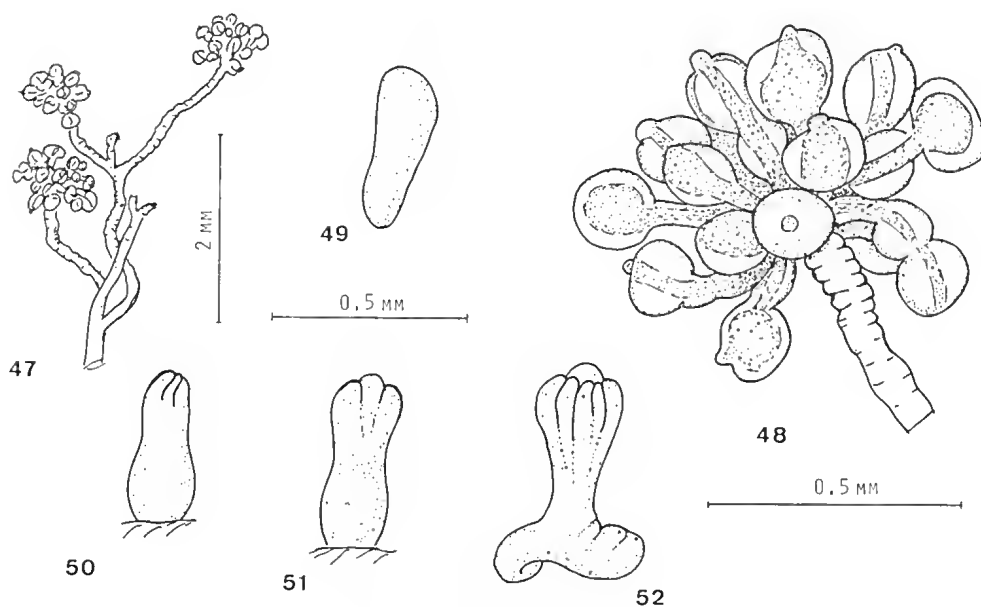
Eudendrium pusilla von Lendenfeld, 1885: 352.

Eudendrium lendenfeldi Briggs, 1922: 150. Rösler, 1978: 104, 120, Pl. 20, Figs. 1-3.

Von Lendenfeld (1885) described two species of *Eudendrium*, *E. generale* and *E. pusilla*, from south-eastern Australia but did not designate a holotype specimen for either species from his type series. Part of the type series of each species is held in the Australian Museum and part in the British Museum (Natural



Figs 40-52—*Eudendrium generale* von Lendenfeld, 1885. 40, Part of stem from microslide BM1886.6.8.38. 41-52, Specimens from Western Port, Vic., drawn from living material. 41, Typical stem with female gonophores. 42, Distal part of branch from same stem showing female gonophores in various stages of maturity. 43, Young female blastostyle before complete loss of tentacles. 44-46, Nematocysts, drawn to same scale. 44, Microbasal eurytele from tentacles. 45, Large microbasal eurytele from hydranth, undischarged. 46, Same, discharged. 47, Part of male colony. 48, Male gonophore cluster. 49-52, Stages in larval development. 49, Newly-released planula. 50, Stage of metamorphosis 12 h after release of planula. 51, Young hydranth 24 h after release. 52, development of hydranth after 48 h.



Figs 47-52—See legend on p. 197.

History). The Australian Museum holdings comprise both microslides and preserved specimens and the British Museum (Natural History) material consists of microslides only. Through courtesy of both museums I have been able to examine and compare the complete type series of both species and it is desirable that a lectotype should now be erected for each. Although von Lendenfeld probably designated his type series from the same colony or from the one collection of material of each species, it is prudent that in erecting lectotypes, only one specimen be nominated from each species.

I therefore designate the following:

Eudendrium generale von Lendenfeld, 1885. Lectotype, AMY203, microslide preparation labelled "*E. generalis* part of type". Lectoparatypes: BM1886.6.8.38, BM1886.6.8.39, microslides labelled "*E. generalis* type"; AMG 9735, spirit-preserved specimen labelled "type" from Port Phillip Bay, Victoria (38° 16' S, 144° 40' E).

Eudendrium pusillum, von Lendenfeld, 1885. Lectotype, microslide labelled "type" AMY204; Lectoparatypes: BM1886.6.8.36a, BM1886.6.8.36c, microslides labelled "*E. pusilla*, type"; AMG 9736, spirit-preserved material labelled "type" from Port Jackson, New South Wales (33° 52' S, 151° 25' E).

The type series of both species is meagre and appears to be the distal fragments of one or several colonies. The condition of the preserved specimens is poor. The stems of specimens in both type series are unfasciated, 0.15 mm in maximum width, and the branches have 3-6 proximal annulations. The male gonophores are 2 or 3-chambered, on a blastostyle devoid of tentacles, distal chamber 0.1-0.5 mm in diameter. Von Lendenfeld noted 24 tentacles on the hydranth of *E. generale* but did not record a number for *E. pusillum*. The lectotype of the latter species also has approximately 24 tentacles. There is no evidence of the ring of "gland cells" (presumably a

nematocyst ring), observed by von Lendenfeld in *E. generale*.

Although all of the extant type material of both species is male, von Lendenfeld described and gave a highly-stylized figure of immature female gonophores of *E. generale*, mistakenly referring to them as the male (see Balch 1919, Kirkpatrick 1890). His figure, therefore, throws little light upon the reproductive structures of *E. generale* other than that the spadix is unbranched and the tentacles are retained on the immature female blastostyle. Although he describes atrophy of the tentacles of the mature blastostyle, the sex of the blastostyle to which he refers cannot be determined from his description. However, from his comments on the colour of the gonophores there is little doubt that he observed living female material, since lost.

A fragment of a hydranth and tentacle of the lectoparatype of *E. pusillum* was examined for nematocysts. Only a few undischarged tentacular microbasic euryteles, capsule $6 \times 3 \mu\text{m}$, were seen. Due to the limited material, no examination could be made of the cnidome of the lectotype of *E. generale*. Despite the lack of a well-preserved cnidome, detailed comparison of the full type series of the two species convinces me that there are no significant differences between the two species. Accordingly, I here synonymize *E. pusillum* with *E. generale*.

Identification of a commonly-occurring, southern Australian hydroid as *E. generale* now permits a full redescription of this species.

MATERIAL AND RECORDS: MVF50526, female colony; coll: J. E. Watson (SCUBA), 2/11/71, depth 6 m. MVF50527, female colony, on the brachiopod *Magellania flavesceus* Lamarck; coll: J. E. Watson (SCUBA), 6/9/78, depth, 10 m. AMG15224, male colony; coll: J. E. Watson (SCUBA), 10/10/81, depth, 9

m. BM1983.8.9.1, female colony; coll: J. E. Watson (SCUBA), 2/11/71, depth, 9 m. All material formalin preserved, from Crawfish Rock, Western Port, Victoria, 38° 20' S, 145° 15' E. AMG15225, male colony, on worm tube, NE of Flinders Island, Bass Strait, 39° 47' S, 148° 13' E, depth 25 m; coll: CSIRO Fisheries Investigations, scallop dredge, 29/7/38 (M. Blackburn).

DESCRIPTION: The following description is based mainly on abundant material from Western Port, Victoria. Colonies up to 40 mm in height, the tallest erect and shrubby, main stems strongly fascicled, smaller colonies up to 20 mm in height, with unfascicled or very lightly-fascicled stems, arising from a tubular hydrorhiza winding over and through the substrate. Unfascicled stems sparsely branched, fascicled stems complexly branched in many planes. Unfascicled stems with 3-8 proximal annulations grading distally into indistinct corrugations, but sometimes smooth.

Hydranths with 24-30 tentacles in a single verticil around a wide, annular hypostome (preserved material), a contraction groove around lower part of most, but not all, hydranths. Gonophores borne over most of colony, thicker in lower parts, male and female on separate colonies. Male gonophores 2 or 3-chambered, borne in a cluster of up to 20 on a blastostyle from which the tentacles are completely absent at all stages, immature distal chamber often with a terminal knob, lost at maturity. Female gonophores very abundant, most on lower part of colony, initially 4-5 immature gonophores with an unbranched spadix, borne on body of a fully-developed hydranth with hypostome. In later stages, the hydranth may continue to grow ahead of the gonophores, or it may be shed; the blastostyle becomes elongated and corrugated, bearing up to 15 gonophores in various stages of maturity. Mature gonophore oval, on a short pedicel, containing a single egg enclosed in a thick gelatinous pellicle.

Nematocysts, microbasic euryteles of two sizes present:

- large, capsule 5-8 × 3-4 µm, shaft 5-7 µm, very abundant in tentacles, on body of hydranth and on female gonophores (Fig. 44).
- larger microbasic euryteles, capsule bean-shaped, variable in size, 13-15 × 7-9 µm, shaft 12 µm (Western Port material), 21-23 µm, shaft 10-12 µm (Flinders Is. specimens), shaft with a few spines; discharges sideways (Figs 45, 46). Moderately common to rare on body of hydranth and nematocyst ring, when present.

MEASUREMENTS, mm: *Stem* (unfascicled) and branches, diameter, 0.12-0.15; *Hydranth*, max. length of pedicel, 1.75, pedicel, distal width, 0.1-0.15, width below tentacles (preserved material), 0.2-0.3; *Gonophores*, max. width of male cluster, 0.75, length of male series, 0.35-0.4, diameter of distal male chamber, 0.2-0.3, max. width of female cluster, 0.88, diameter of mature female, 0.28-0.3.

COLOUR: Overall colour of reproductive colonies, orange; stems brown, hydranths pink to orange, tentacles paler pink; male gonophores pearly pink, spadix

orange; female gonophores brilliant orange to scarlet.

REMARKS: The colonies of *E. generale* from the Bass Strait region (including Western Port and Flinders Is.) are short and usually unfascicled at early maturity. Heavily-fascicled colonies from Western Port are probably quite old, and it is suspected that the hydrorhizal filaments and main stems of these colonies may exist over several seasons (pers. obs.). While the Flinders Is. specimens are similar in colony morphology with the younger unfascicled, or lightly-fascicled colonies on brachiopod shells from Western Port, the supplementary microbasic euryteles of the Flinders Is. specimens are much larger than those from Western Port. However, the length-width ratio remains the same throughout the material examined, ranging from 1.7-1.9:1.

Examination of the cnidome was carried out on abundant living material of *E. generale*. In mature colonies, the large supplementary microbasic euryteles were present in the nematocyst ring ("gland cells" of von Lendenfeld) around the body of young, unproductive hydranths on the distal branches. They occurred on only 25% of these hydranths and were never associated with the hypostome. As the hydranth becomes fertile the supplementary nematocysts move outwards in scattered groups on the surface of the developing gonophore. They are, however, never aggregated into nematocyst pads. When lost, the nematocysts are not replaced, so that by maturity, none remain on the gonophore. These observations are not in agreement with Mergner (see Rösler, 1978 p. 86) who considers that nematocyst pads on the female gonophore are characteristic of *E. generale*. Problems in separation of *E. generale* from *E. capillare* have been pointed out by Vervoort (1941) and by Nutting (1896) in discussion of *E. album*. Rösler (1978) also admits difficulty in distinguishing *E. generale* from *E. speciosum* Fraser, 1945. The problem of distinguishing morphologically-similar species from *E. generale* is compounded by the fugitive behaviour, and variations in relative abundance, of the supplementary nematocysts of *E. generale*. Failure to detect the larger microbasic euryteles would then lead to confusion of small colonies of *E. generale* with *E. capillare*, even if the material were fertile.

Pennycuik (1959) was uncertain whether her small sterile colonies from Currumbin, Queensland, were *E. generale* or *E. capillare*. Examination of her specimens, loaned by the Queensland Museum, revealed the presence of abundant heteronemes, demonstrating that her material is neither of these species. This material is described elsewhere in this paper (p. 209). Bale (1884) briefly described, but was unable to clearly identify a small specimen of *Eudendrium* from Portland, Victoria. His comments, and observations by the present author, suggest that his specimen was probably *E. generale*. I have also examined a series of microslides labelled 1959.33.129-135, Station 22, Mergui Archipelago, identified by Ritchie (1910) as *E. generalis* von Lendenfeld, kindly loaned by the Royal Scottish Museum, Edinburgh. Although the material is rather impoverished and difficult to diagnose in the thick Canada Balsam moun-

tant, some undischarged nematocysts are reasonably clear. The tentacular microbasic euryteles measure $10\text{--}11 \times 4\text{--}5 \mu\text{m}$, and the supplementary microbasic euryteles measure $25\text{--}28 \times 10\text{--}13 \mu\text{m}$. Although the kind of cnidome agrees with that of *E. generale*, both the tentacular and supplementary microbasic euryteles are larger, having a capsular length-width ratio of 2.4:1 for both sizes of nematocysts. This ratio is greater than those in *E. generale* from Australia (1.8:1, tentacular, and 2:1, supplementary nematocysts). Further, the partially-reduced tentacles of the mature female blastostyle show that the Mergui specimens cannot be *E. generale*; they may, however, be *E. capillare* as described by Millard (1975) and by Vannucci (1954). Until the male gonophore of the Mergui species is found, the identity of Ritchie's species remains uncertain.

Hargitt (1927), in referring a specimen from Amoy in the South China Sea to *E. pusillum* var. *amoyicum*, considered that the differences exhibited by the varietal form might eventually warrant its separation as a new species. I have examined a microslide labelled "type of *E. pusillum* var. *amoyicum*" kindly loaned by the Smithsonian Institution (USNM 42637). The specimen is a mature unfasciated and branched female stem. It is very similar to *E. generale* although distinctly smaller in size. It is not well preserved, but the endome is sufficiently clear to show abundant small tentacular microbasic euryteles and a few larger microbasic euryteles, none of which are discharged. Capsular dimensions of the latter nematocysts are, length, $20 \mu\text{m}$, and width, $10 \mu\text{m}$. Ling (1938) described a male colony of the var. *amoyicum* from the Chushan Islands. The gonophores are borne on a blastostyle without tentacles. This evidence confirms the close relationship of var. *amoyicum* with *E. generale*. However, the much smaller size of the colonies suggests that further study should be made of fresh material before a decision is made as to its systematic status. For the present, the South China Sea material is regarded as probably a distinct species.

REPRODUCTION: Colonies from Western Port, Victoria, released planulae in the laboratory aquarium. The elongate planulae descend on mucous strings and crawl slowly away from the parent colony in the manner described in *E. rameum* by Wasserthal and Wasserthal (1975). Over a period of 12 h the planulae metamorphosed to a dumb-bell shape, aboral pole down, the upward-facing oral pole showing a trace of differentiation of tentacles. Between 24–48 h, a young hydranth 0.5 mm in height with hypostome surrounded by embryonic tentacles began to develop. At this stage the aboral pole extended each side of the peduncle as a rudimentary hydrorhiza. Observations were terminated after 48 h.

Although young colonies of *E. generale* are small and relatively inconspicuous, the brilliant orange to scarlet colour of mature colonies, remarked upon by von Lendenfeld, is unmistakable in the field. Under favourable conditions *E. generale* forms dense meadows on sponges and ascidians, often sharing its habitat with another hydroid described as a new species later in this paper (p. 205). Young, lightly-fasciated colonies occur

on pebbles and on old shells in shallow water while the more luxuriant older colonies are usually confined to deeper waters. *Eudendrium generale* is fertile from late spring (September) to autumn (April).

DISTRIBUTION: From Portland, Victoria (pers. obs.) to temperate New South Wales.

Eudendrium merulum n. sp.

Figs 53–58

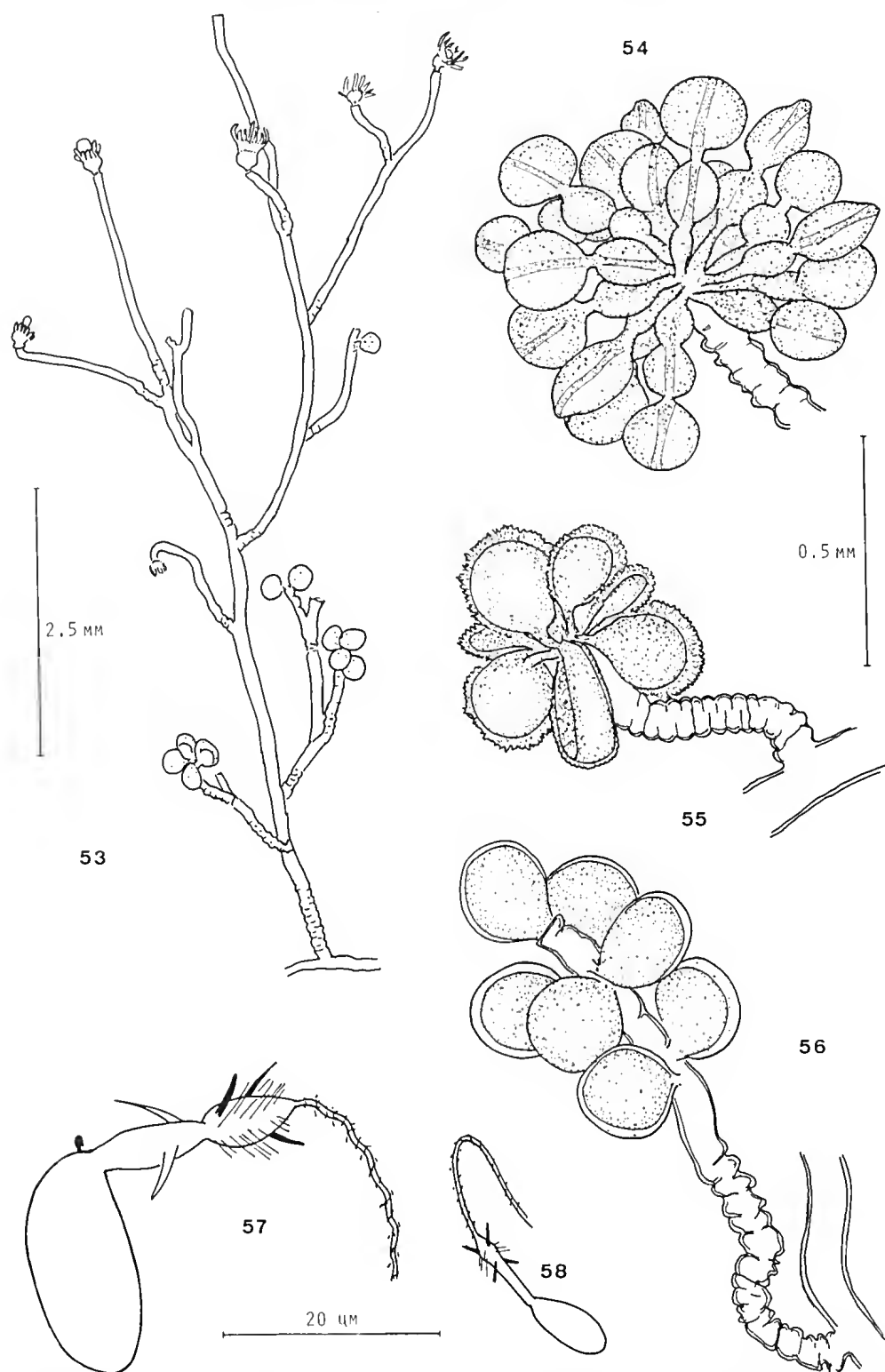
TYPE MATERIAL AND RECORD: Holotype, MVF50514, female colony. Paratypes, MVF50515, female colony; MVF50516, female colony; MVF50517, male colony. All material alcohol preserved, 0.5 km south of Clonmel Island, Bass Strait, Victoria, $38^\circ 45' \text{S}$, $146^\circ 43' \text{E}$, from wreck of steamer "Blackbird", depth, 6 m; coll: J. E. Watson (SCUBA), 16/3/83. Other material; MVF50518, male colony, formalin preserved, coral reef, 2 m deep, Palm Isles, Queensland, $18^\circ 40' \text{S}$, $146^\circ 30' \text{E}$; coll: J. E. Watson (SCUBA), 28/6/73.

DESCRIPTION FROM HOLOTYPE AND PARATYPES: Hydro-rhiza tubular, giving rise to simple or branched stems of the same diameter. Stems erect, up to 20 mm in height, unfasciated, lower stems roughly annulated up to the lowest branch, branching and rebranching sparse and irregular, in all planes, branches straight or undulated, upwardly directed, with up to 12 indistinct proximal annulations. Perisarc of lower stems thick and shining, becoming markedly thinner in distal region.

Hydranth small, with approximately 24 tentacles surrounding a club-shaped hypostome (preserved material) and a distinct contraction groove around the base below a nematocyst ring containing a few large nematocysts. Sexes borne on separate colonies. Female gonophores borne thickly, on lower parts of colony, clusters extending to halfway up stems, immature gonophores disk-shaped with a curved, unbranched spadix, in a verticil surrounding a hydranth without hypostome. Mature female gonophore globular, containing one egg enclosed in a thin pellicle, up to 6 gonophores scattered along a wrinkled blastostyle devoid of tentacles. Male gonophores borne on lower stems, in a dense cluster of up to 20 on a wrinkled blastostyle completely devoid of tentacles at all stages. Gonophores 2 or 3-chambered, the chambers connected by a distinct neck; immature gonophores elongate, some with an apical knob, mature gonophores bead-shaped.

Nematocysts, microbasic euryteles of two sizes present:

- large microbasic euryteles, capsule bean-shaped, $19\text{--}23 \times 9\text{--}12 \mu\text{m}$, shaft discharging sideways, about $20 \mu\text{m}$ long, rather delicate and easily collapsed, armed with numerous spines and bristles, thread rosy (Fig. 57). Present around hypostome, in the nematocyst ring on the hydranth and grouped circumferentially on spadix of female gonophore.
- small microbasic euryteles, capsule $7\text{--}9 \times 3 \mu\text{m}$, shaft $7\text{--}9 \mu\text{m}$, long and thin with at least two sets of spines on head, the distal spines facing forward. Abundant on tentacles (Fig. 58).



Figs 53-58—*Eudendrium merulum* n. sp. 53, Whole stem from holotype, Bass Strait, Vic. 54, Mature male gonophores from paratype colony. 55, 56, Female gonophores from holotype. 55, Immature gonophores. 56, Mature gonophores. 57, 58, Nematocysts, drawn to same scale. 57, Large microbasic eurytele from hypostome, discharged. 58, Small microbasic eurytele from tentacles.

MEASUREMENTS, mm: *Stem* and *branches*, width, 0.08-0.11; *Pedicle*, distal width, 0.08-0.1; *Hydranth*, (preserved material) width below tentacles 0.13-0.18; *Gonophores*, female, diameter of cluster, 0.6-0.7, max. mature diameter, 0.28, male, max. diameter of distal chamber, 0.2.

COLOUR: Lower stems dark brown, becoming almost colourless distally below hydranth. Hydranths flesh coloured to orange, female gonophores orange, spadix of immature gonophore white to purplish; male gonophore pearly or clear, spadix yellow, brown or orange.

REMARKS: Colonies of *E. merulum* are indistinguishable in the field from *E. generale* von Lendenfeld, 1885. In microscopic characters the species is, however, easily differentiated from *E. generale* by the larger size of the microbasic euryteles and the complete absence of tentacles from the mature male and female blastostyles. The tentacular nematocysts proved to be very difficult to discharge, even in living material.

Eudendrium merulum is a small hydroid which prefers a shaded microhabitat in good current flow, and particularly favours situations where edge effects (Foster 1975) are dominant. Under these conditions it forms extensive hydroid meadows.

OTHER MATERIAL: The Queensland material is limited, comprising one small colony which shows some variation from the type series in size of nematocysts and atrophy of the tentacles of the male blastostyle. For this reason it is described separately. The colonies are shorter than those of the type material, being up to 10 mm in height. While other colony characters are similar, the stem and branches are thicker (0.13-0.2 mm), there are fewer proximal annulations (2-4) on the branches, and occasionally there are groups of corrugations about midway along the branches. The immature male gonophores are 2-chambered, borne on a blastostyle with fully-developed tentacles. This condition contrasts with the type specimen where the tentacles of the male blastostyle are completely absent at all stages of development.

The tentacular microbasic euryteles are similar in size to those of the type, the capsule being $7.8 \times 3.4 \mu\text{m}$ and the shaft $7.9 \mu\text{m}$ long, with a very thick thread. The hypostomal nematocysts are slightly longer than those of the type, the capsule being $22.23 \mu\text{m} \times 10.11 \mu\text{m}$, shaft $16.20 \mu\text{m}$ long, also with a thick, ropy thread. The length-width ratio is, however, similar, the ratio of the type being 1.9-2.1:1, while that of the Queensland specimens is 2.1-2.2:1. Until further tropical material is available for study, the Queensland specimen is provisionally assigned to *E. merulum*.

ETYMOLOGY: The species is named after the wreck of the steamer "Blackbird", off Port Albert, Victoria.

Eudendrium carneum Clarke, 1882

Figs 59-62

Eudendrium carneum, Clarke, 1882: 137, Pl. 7, Figs 10-17. Vannucci, 1954: 101, Pl. 1. Figs 1-9, Pl. 2,

Fig. 8, Pl. 4, Figs. 2-5. Millard, 1959: 302, Fig. 1A-F.

Vervoort, 1968: 8. Rösler, 1978: 55, Pl. 9, Figs 1-6. MATERIAL AND RECORDS: WAM95-1957, two female colonies, alcohol preserved, South Mole, Fremantle, Western Australia, $31^{\circ} 55' \text{S}$, $115^{\circ} 45' \text{E}$, from wharf pile (no depth); coll: B. R. Wilson, March, 1957. MVF50724, two female colonies, alcohol preserved, North Mole, Fremantle, Western Australia, depth 6m; coll: J. E. Watson, 25/11/83.

DESCRIPTION: All specimens are large arborescent colonies reaching a height of 18 cm. The colonies from South Mole are richly branched and bear very young female gonophores. Those from North Mole are senescent and overgrown by algae and other hydroids. One colony bears female gonophores in various stages of development. Mains stems thick, gnarled and heavily fasciated, the fasciculations extending to all but the growing tips of the colony and along the primary branches. Branching profuse, irregular, each branch with 4-7 deep proximal annulations, the younger branches sometimes with scattered groups of annulations, perisarc otherwise smooth, thick and shining.

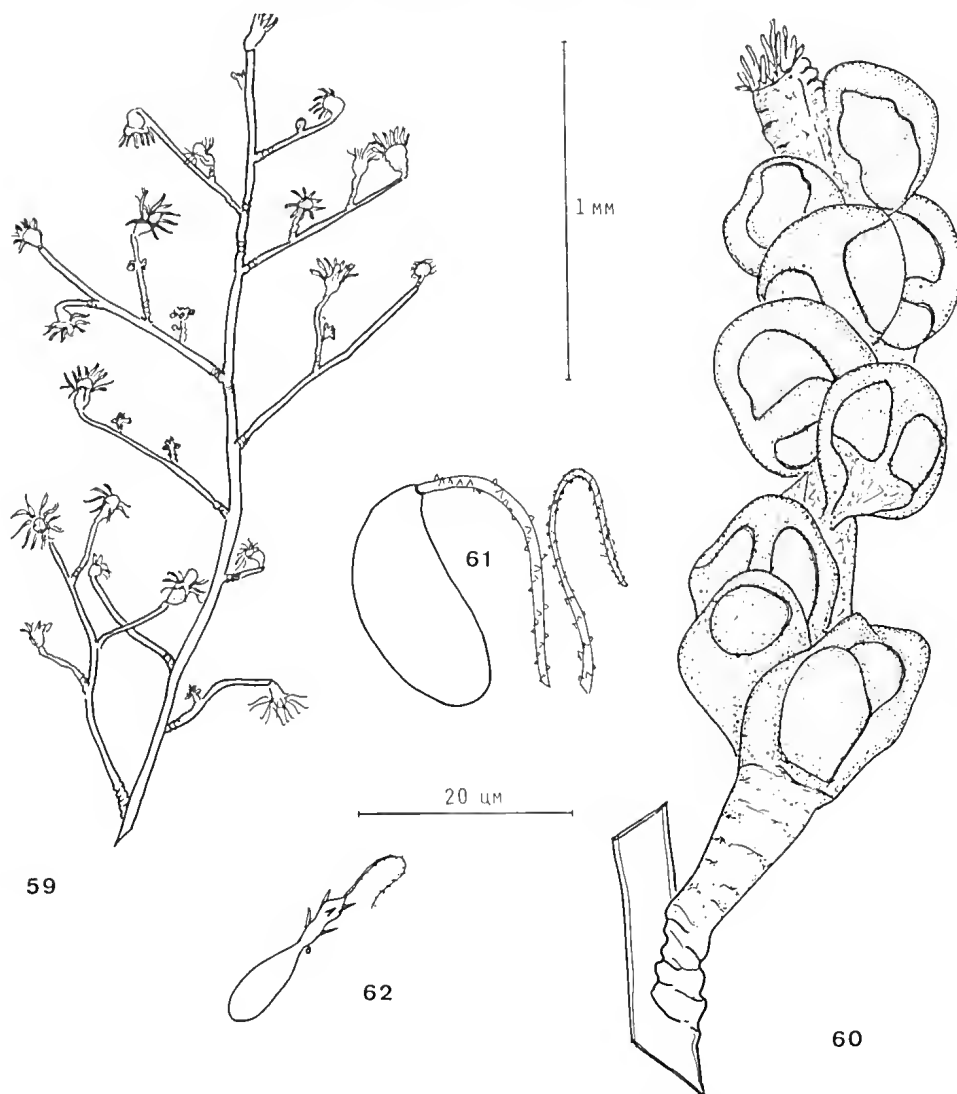
Hydranths large, of elegant form, with a long body and 28-32 tentacles, a very prominent clavate hypostome (preserved material), and a distinct contraction groove at base. Female gonophores borne on a specialised blastostyle on a short wrinkled pedicel arising from the smaller branches. Immature gonophores small, knob-like, 4-6 borne in a whorl below a hydranth with 10-14 atrophied tentacles; gonophores later developing a bifurcated spadix. Mature gonophores in elongate clusters of 5-8 scattered along a thickened blastostyle which may be surmounted by a cluster of remnant tentacles without hypostome, each gonophore enclosed in a capsule of perisarc with two large fenestrations.

Nematocysts of two kinds present:

- large heterotrichous anisorhizas, capsule loaf-shaped, $20.22 \times 9.11 \mu\text{m}$, thread very long (up to 1 mm), $1.3 \mu\text{m}$ wide proximally, armed with thorn-like spines, tapering distally to $0.5 \mu\text{m}$ diameter, the spines becoming smaller and more closely spaced distally (Fig. 61). Very abundant on body of hydranth, in nematocyst ring, on spadix of immature gonophore and scattered on body of the mature gonophore.
- microbasic euryteles, capsule pyriform, $8.9 \times 3 \mu\text{m}$, shaft $6 \times 2 \mu\text{m}$ with several long spines, thread moderately long with small bristle-like spines (Fig. 62). Moderately abundant in tentacles.

MEASUREMENTS, mm: *Main stem*, max. width, 7-8; *Main branches*, max. width, 0.25; *Distal branches*, proximal width, 0.1-0.18; *Hydranth* (preserved material), length of body, 0.3-0.4, width below tentacles, 0.3-0.4; *Mature gonophore*, length, 0.35-0.4; width, 0.3-0.35.

REMARKS: The colonies correspond exactly to the description of *Eudendrium carneum* given by Millard (1959) for specimens from the east coast of South Africa. The large, strongly-fasciated colonies, the bifurcated female spadix and the fenestrate capsule of the



Figs 59-62—*Eudendrium carneum* Clarke, 1882. 59, Distal part of branch from female colony from Fremantle, W.A. 60, Female blastostyle with mature gonophores surmounted by a reduced hydranth. 61, 62, Nematocysts, drawn to same scale. 61, Large heterotrichous anisorhiza from hydranth. 62, Microbasie eurytele from tentacles.

mature female gonophore readily distinguish this species from all others. Examination of the endime of freshly-collected material shows the larger nematocysts to be heterotrichous anisorhizas, not atrichous isorhizas as reported by Millard (1959). When undischarged, the relatively short distal end of the thread is obscured by the loose proximal coils in the capsule, and is thus easily overlooked. Most of the colonies appear to be quite old, many of the branches showing evidence of breakage, most likely due to fish grazing, followed by regeneration. Each regeneration commences with a few deep annulations. Many of the fascicular tubes on the stem and branches show a downwardly growing tip, suggesting that the strongly-fascicled habit of the colonies may be a result of gregarious larval settlement on the colony rather than upward growth from the parent rootstock.

The colonies from Western Australia are pale orange in life, not brilliant vermillion as reported for American specimens by Clarke (1882).

Eudendrium carneum is known from the Atlantic and Pacific coasts of North America, the north-eastern coast of South America, St. Helena, southern Africa and the tropical east Pacific. The Australian record of *E. carneum* is from wharf pilings and on rocks at the entrance to the Port of Fremantle, where it has been established for at least 26 years. This is a similar habitat, associated with shipping, to that recorded from Durban in east Africa by Millard (1959). Other records probably associated with shipping are the Suez Canal, the Hampstead Roads, Virginia, U.S.A. (Clarke 1882) and Santa Marta, Colombia (Wedler 1975).

This is a new record for Australia and the east Indian Ocean.

Eudendrium racemosum (Cavolini, 1785)

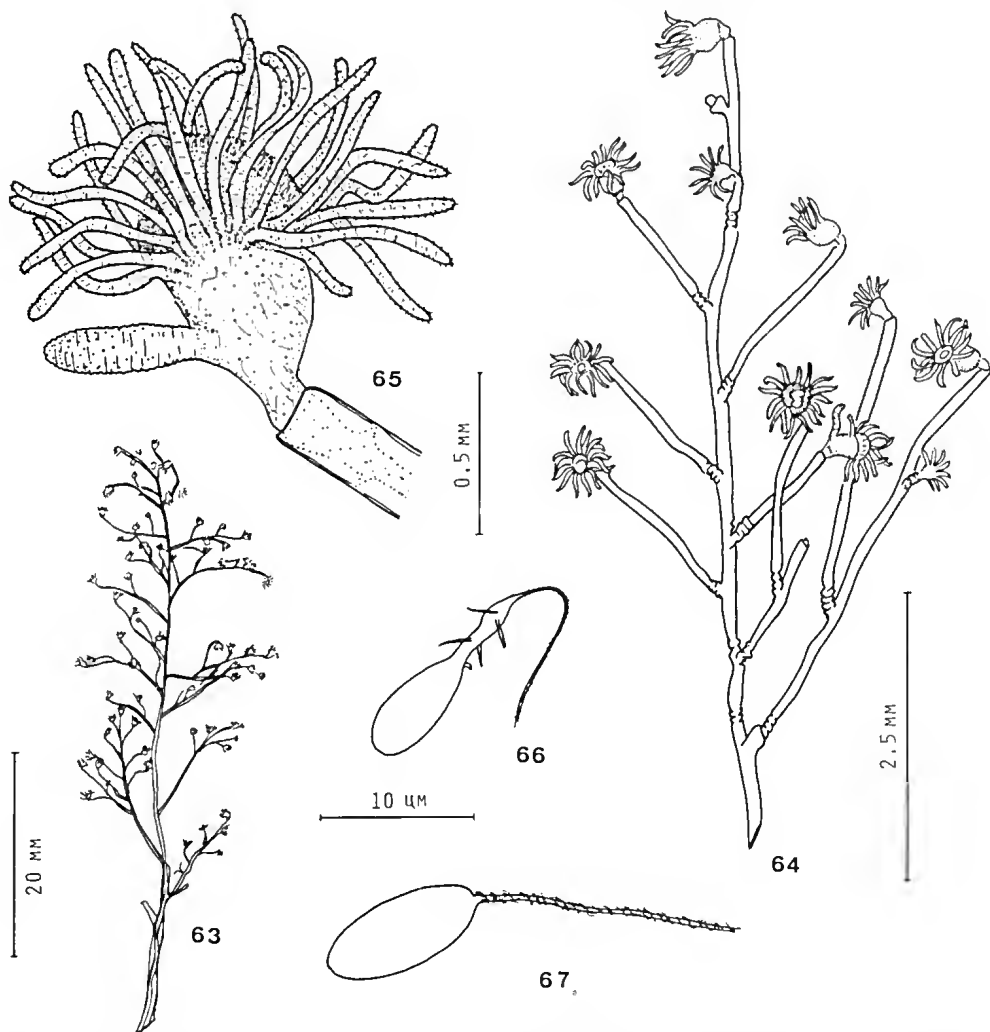
Figs 63-67

Sertolara racemosa Cavolini, 1785: 160, Pl. 6, Figs. 1-7, 14, 15.*Sertularia racemosa* Gmelin, 1788-93: 3854. Sprengel, 1813: 73, Pl. 6.

Eudendrium racemosum Ehrenberg, 1834: 296. Alder, 1856: 356. Allman, 1864a: 387, 407; 1871: 148, 341. Weismann, 1881: 1, Pl. 1, Figs. 1-8. Von Lendenfeld, 1885: 351, 353. Schneider, 1879: 477. Hargitt, 1900: 240; 1904: 259, Pl. 14, Fig. 1. Billard, 1904: 103. Hartlaub, 1905: 551. Motz-Kossowska, 1905: 53. Stechow, 1920: 32; 1923a, 83; 1923b: 4. Picard, 1955: 183. Mergner, 1957: 63, Figs. 1-96, Pl. 1. Riedl, 1959: 621. Hanisch, 1970: 1, Figs. 1-45. Millard & Bouillon, 1973: 33. Rösler, 1978: 123, Pl. 22, Figs. 1-4.

MATERIAL AND RECORDS: MVF50519, one sterile colony, formalin preserved, from reef, 25 m deep, Stradbroke Is., Queensland, 27° 20' S, 153° 35' E; coll: J. E. Watson (SCUBA), 24/8/75. MVF51783, female colonies, alcohol preserved, coral reef, 6 m deep, Raine Is., Queensland, 11° 36' S, 144° 1' E; coll: A. L. Ayling (SCUBA), 9/4/84.

DESCRIPTION: Colonies of moderate height, ranging from 30-70 mm, main stems unfasciated or with one supplementary fascicular tube. The colony from Stradbroke Is. is irregularly branched in several planes around stem; those from Raine Is. show a tendency towards a more planar habit. Primary branches long, particularly those in the proximal stem region, secondary branches bearing hydranth pedicels. Branches with a few spiral annulations at origin; groups of annulations sometimes at irregular intervals along branch, perisarc otherwise smooth. Hydranths large, with an open trumpet-shaped



Figs 63-67 — *Eudendrium racemosum* (Cavolini, 1785). Colony from Stradbroke Island, Qd. 63, Whole stem. 64, Distal end of branch. 65, Hydranth with cnidophore. 66, 67, Nematocysts, drawn to same scale. 66, Microbasic eurytele, undischarged, from tentacles. 67, Atrichous isorhiza, discharged, from cnidophore.

and sometimes fluted hypostome (preserved material), surrounded by 27-30 tentacles, a contraction groove and an indistinct nematocyst ring in the proximal region. A cnidophore (Weismann 1881) present in 20% of hydranths, arising just above the contraction groove, usually on hydranths in the proximal region of the branch. The cnidophore is usually thicker than the tentacles and often several times the length of the hydranth, the distal end thickly armed with nematocysts. Female gonophores borne in clusters of up to 10 on a wrinkled blastostyle below a hydranth with a reduced number of partially-atrophied tentacles. Spadix of female bifurcated in early stages of development, the bifurcation remaining until the egg reaches maturity.

Nematocysts of two kinds present, none discharged:

- small microbasic euryteles, capsule $6.5-7 \times 2-3 \mu\text{m}$, shaft $5-6 \mu\text{m}$, very abundant in tentacles (Fig. 66).
- atrichous isorhizas, capsule bean-shaped, $9-11 \times 3.5-4 \mu\text{m}$ wide, thread moderately long, finely spinous, loosely coiled inside capsule when undischarged (Fig. 67). Moderately common around hypostome and very abundant on cnidophore.

MEASUREMENTS, mm: *Stem*, max. width, 0.75; *Branch*, max. length, 25, width of branch and pedicel, 0.15-0.23; *Hydranth* (preserved material), width below tentacles, 0.25-0.6.

REMARKS: *Eudendrium racemosum* is known from the Mediterranean Sea (Mergner 1957), the Seychelles (Millard & Bouillon 1973), Vietnam (Leloup 1937) and Japan (Stechow 1913, Yamada 1959, Hirohito 1969). This is the first record from the South Pacific region. The species is probably widely distributed throughout the Australian tropics, the two present records being from the northern and the southern extremes of the Great Barrier Reef.

Eudendrium balei n. sp.

Figs 68-74

non Eudendrium generale von Lendenfeld, 1885. Bale, 1919: 335. Watson, 1982: 89, Fig. 4.6j, Pl. 10.3.

TYPE MATERIAL AND RECORDS: Holotype, MVF50521, female colony, formalin preserved, Crawfish Rock, Western Port, Victoria, $38^{\circ} 20' \text{S}$, $145^{\circ} 15' \text{E}$, depth, 10 m; coll: J. E. Watson (SCUBA), 2/11/71. Paratypes: MVF50522, female colony, formalin preserved, Crawfish Rock, Western Port, depth, 10 m; coll: J. E. Watson (SCUBA), 13/9/68. MVF50530, male colony, formalin preserved. Crawfish Rock; coll: J. E. Watson, 10/10/81. MVF50523, male colony, from reef 15 m deep, Seaspray, Victoria, $38^{\circ} 30' \text{S}$, $147^{\circ} 10' \text{E}$; coll: J. E. Watson (SCUBA), 27/10/81. MVF50720, sterile stem, Stn 20, Museum of Victoria Survey, Bass Strait, Victoria, $37^{\circ} 59' \text{S}$, $148^{\circ} 27' \text{E}$, depth 51 m; trawl, 1/7/83. Bottom, muddy sand, fine shell.

OTHER MATERIAL: MVF50525, Gabo Is., Victoria $37^{\circ} 35' \text{S}$, $149^{\circ} 55' \text{E}$, depth, 6m; coll: J. E. Watson (SCUBA), 15/2/73. MVF50524, from experimental

fouling panels, Sydney Harbour, New South Wales, $33^{\circ} 50' \text{S}$, $151^{\circ} 15' \text{E}$; coll: G. Russ, January 1974.

DESCRIPTION FROM HOLOTYPE AND PARATYPES: Colonies up to 10 cm in height. Hydorrhiza a tangled mass of tubes, becoming erect at intervals as stems. Stems more or less straight, perisarc thick, smooth, shining, fascicled to about halfway up colony, primary branches long, of same diameter as stem, given off irregularly or in an irregular whorl in three planes at an acute angle to stem. Rebranching common, repeated up to 5 times, each branch commencing with up to 7 distinct annulations, minor branches and hydranth pedicels often indistinctly corrugated throughout their length. Hydranth pedicels long, perisarc usually terminating sharply well below hydranth, but sometimes grading into hydranth. Hydranths large, with 20-24 tentacles surrounded by a wide hypostome; usually a contraction groove near base. Sexes on separate colonies, male and female gonophores borne on all parts of colony except the most distal branches. Male gonophore 3-chambered, in clusters of up to 12 on a wrinkled pedicel below a fully-formed hydranth, immature gonophore with a tiny apical tubercule, lost at maturity, distal chamber of mature gonophore bun-shaped with inflated spadix. Female gonophores borne below a fully-developed hydranth with a hypostome and a reduced number of tentacles (see remarks), up to 20 gonophores in various stages of maturity scattered along a wrinkled blastostyle. Immature gonophores large, spadix unbranched, with scattered clusters of nematocysts. Mature gonophore egg-shaped, on a short pedicel, containing a single egg enclosed in a very thin transparent pellicle.

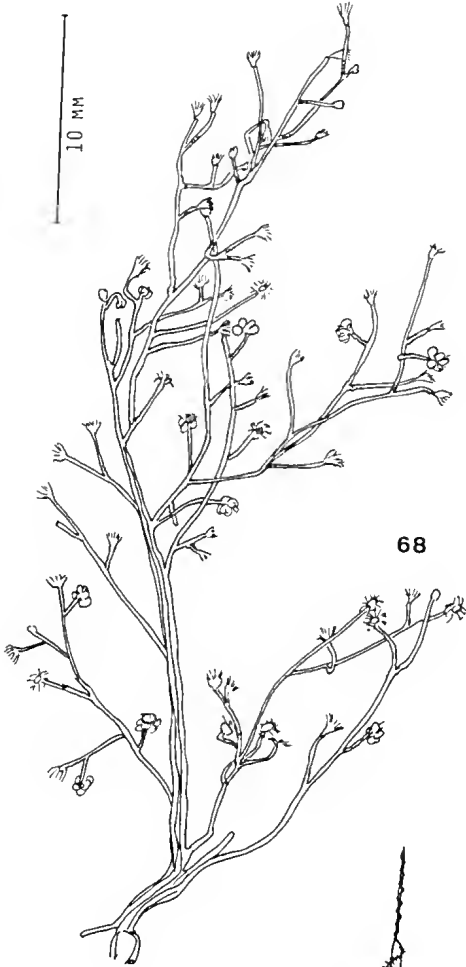
Nematocysts of two kinds present:

- microbasic euryteles, capsule $8-10 \times 4-5 \mu\text{m}$, shaft $7 \mu\text{m}$ long, with several large spines (Fig. 71). Very abundant in tentacles.
- microbasic mastigophores, capsule bean-shaped, $19-22 \times 10 \mu\text{m}$ long, $1.5 \mu\text{m}$ thick, thread $400 \mu\text{m}$ long, thick and spinous (Fig. 72). Moderately common on hypostome, sometimes on body of hydranth and in clusters on spadix of immature female gonophore.

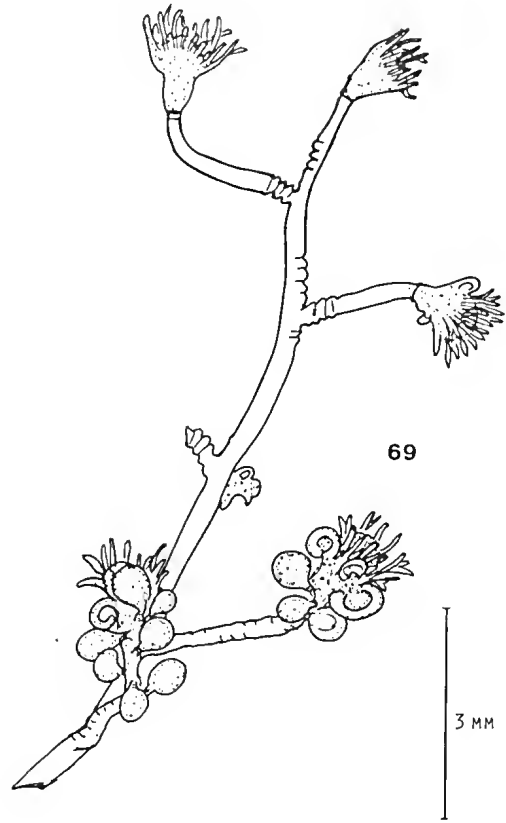
MEASUREMENTS, mm: *Stem* and *branches*, max. diameter, 0.4, Primary branches, max. length, 10.0; *Hydranth*, max. length of pedicel, 1.5, pedicel, distal width, 0.25-0.33, max. width of body below tentacles (preserved material), 0.67, max. width across tentacles (living material), 2.5, width across body (living material), 1.0; *Gonophores*, max. length mature male series, 0.65, diameter of mature distal chamber, 0.3-0.38, diameter of mature female, 0.45-0.5.

COLOUR: Perisarc of older stems shining dark brown, lighter in younger parts of colony. Body of hydranth orange, tentacles pink, male gonophores pearly pink, spadix deep orange; female gonophores brilliant orange. Overall colour of colony, orange to pink.

REMARKS: *Eudendrium balei* is similar in size and habit to *E. lineale* Yamada, 1954, *E. japonicum* Yamada, 1954 (known to me only from the literature), and to certain growth forms of *E. ramosum* (Linnaeus, 1758)



68

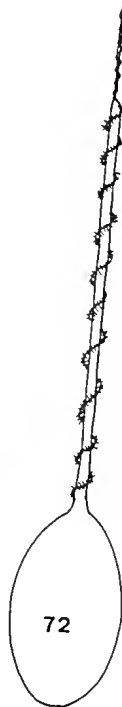


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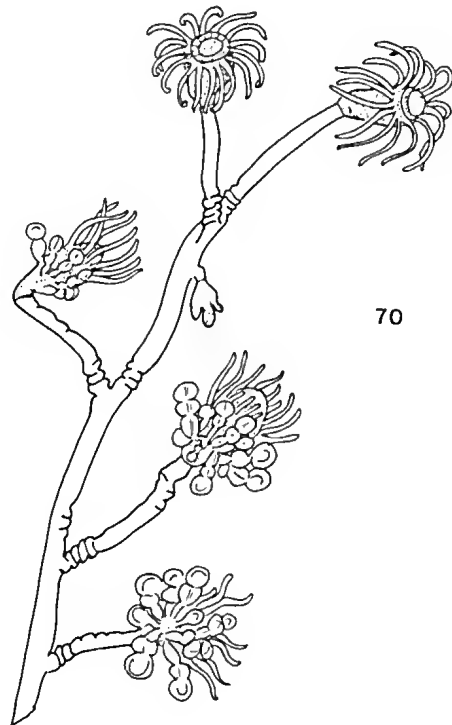


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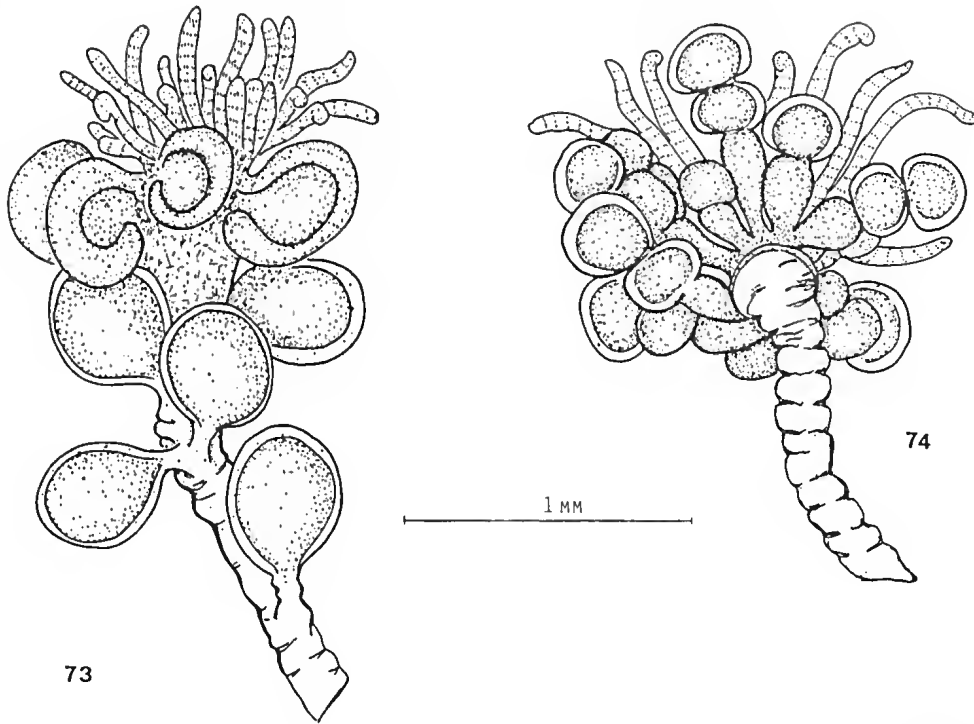
20 μ m



72



70



Figs 68-74—*Eudendrium balei* n. sp. 68, Single stem from holotype, Western Port, Vic. 69, Distal part of branch with female gonophores, from holotype. 70, Distal part of branch with male gonophores, from paratype. 71, 72, Nematocysts, drawn to same scale. 71, Microbasic eurytele from tentacles. 72, Microbasic p-mastigophore from hydranth. 73, Female blastostyle from holotype with gonophores in various stages of maturity. 74, Mature male blastostyle from paratype.

(Millard 1975). The male gonophores of the first two species are, however, borne on blastostyles without tentacles, and the tentacles of the female blastostyle of *E. ramosum* are lost at maturity, not partly retained as in *E. balei*. On the other hand, Fraser (1944) figures the female blastostyle of *E. ramosum* with only partly-atrophied tentacles. Following Mariscal (1974), the supplementary nematocysts of the endome are here classified as microbasic p-mastigophores.

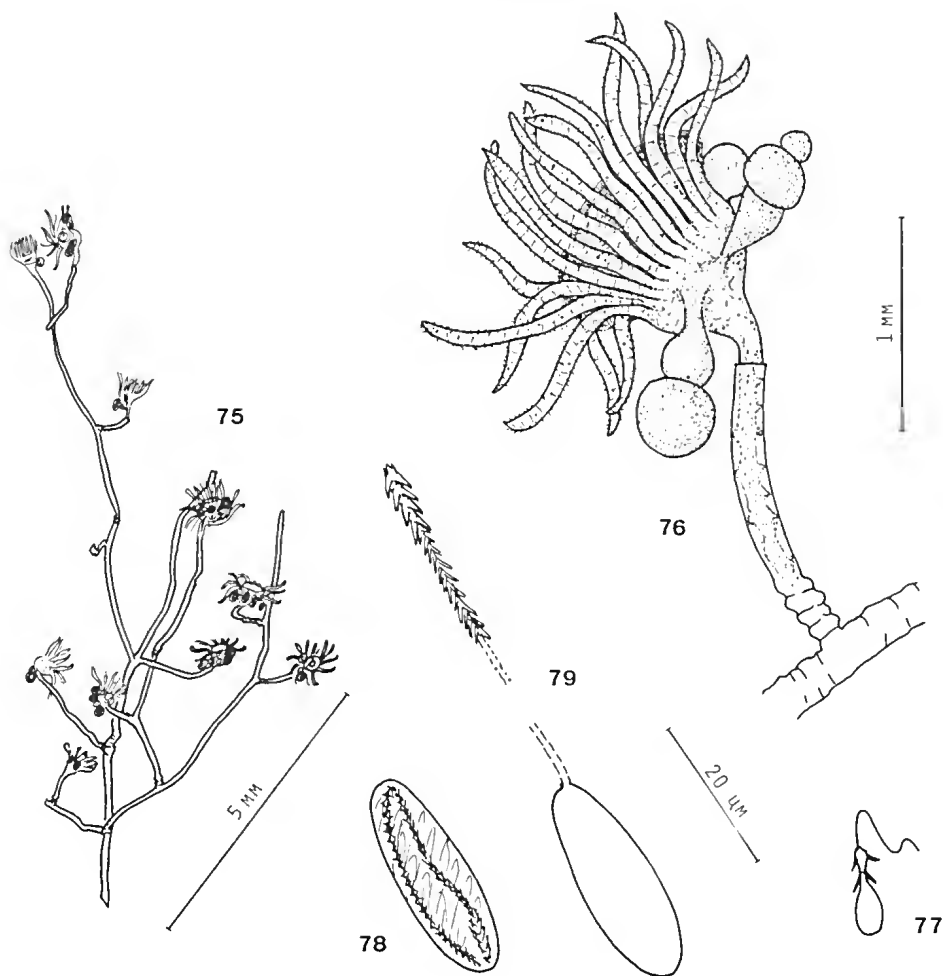
The hydroid from Port Phillip Bay, Victoria, assigned to *E. generale* von Lendenfeld, 1885 by Bale (1919) is clearly not that species but an immature female colony of *E. balei*. Bale refers to the "gland cells" on the hydranth and "nematocyst pads" on the gonophores. These occur in *E. balei* but there are no nematocyst pads on the gonophores of *E. generale*. Their occurrence in *E. balei* is usually in scattered groups rather than aggregated in pads, and only on the immature female gonophore. The microbasic mastigophores are very abundant on the hydranth, especially around the hypostome. When fully discharged, the shaft bears a spiral of fine bristles, the thread is very long and straight and it is armed with very fine, scarcely discernible bristles. *Eudendrium balei* forms large, robust and conspicuous colonies which, under favourable conditions, may grow up to 15 cm high and 20 cm wide. It is fertile from October to May (spring to early winter).

DISTRIBUTION: Known at present from Victoria (cool temperate) to the central New South Wales (warm temperate) coastline.

ETYMOLOGY: The species is named after W. M. Bale, an early authority on Australian Hydroida, who first recorded it from Port Phillip Bay.

LABORATORY OBSERVATIONS: Abundant fresh material of *E. balei* has permitted some observations on reproductive behaviour of the species. While the mature female blastostyle usually bears the same number of tentacles as the unreprouductive hydranth, only half of these are ever fully extended to their normal length, each alternate tentacle being reduced to a club-shaped vestige. This type of retraction (or atrophy) of the tentacles never occurs on the sterile hydranths of the rest of the colony. Shrinkage of alternate tentacles to half the normal complement is necessary to provide space for the remaining tentacles and the developing gonophores. In contrast, tentacles of the male blastostyle never show any tendency toward reduction in number or size.

Release of planulae was also observed. The newly-released planula is 0.5 mm in length and descends from the parent colony on a mucous string in the same manner as that described in *E. generale*. Upon contact with a firm surface the planula elongates and crawls sluggishly away from the parent colony. Metamorphosis had not occurred after 48 h when observations were terminated.



Figs 75-79—*Eudendrium aylingae* n. sp. Drawn from holotype colony, Great Detached Reef, Qd. 75, Whole stem. 76, Hydranth with male gonophores. 77-79, Nematocysts, drawn to same scale. 77, Microbasie eurytele from tentacles. 78, Macrobasie eurytele, undischarged, from hypostome. 79, Macrobasie eurytele, discharged, showing overlapping distal spines on shaft.

***Eudendrium aylingae* n. sp.**

Figs 75-79

TYPE MATERIAL AND RECORDS: Holotype, MVF50529, one male colony, formalin preserved, Great Detached Reef, Queensland, 11° 58' S, 143° 58' E (no depth recorded); coll: A. L. Ayling (SCUBA), 22/5/79.

OTHER MATERIAL: MVF50722, microslide (Berlese mountant), Museum of Victoria Bass Strait Survey, Stn 155, 70 m, 38° 56' S, 145° 16.6' E, "Tangaroa" Cruise 81-T-1, 12/11/81. MVF50723, one male colony, alcohol preserved, Whitfords Reef, Perth, Western Australia, 31° 55' S, 115° 45' E, depth, 12 m; coll: J. E. Watson (SCUBA), 22/11/83.

DESCRIPTION OF HOLOTYPE: One colony fragment 12 mm in height, without substrate. Colony erect with no definite main stem. Branching irregular, branches straggling, with 3-4 indistinct annulations at origin and at irregular intervals throughout; stems otherwise smooth

and shining, perisarc thin. Hydranths terminal on branches or borne on irregularly-spaced pedicels, indistinctly annulated at origin. Hydranths moderately large with a wide hypostome (preserved material) and 20-22 tentacles. Male gonophores 2-chambered, up to 5 borne on a fully-developed hydranth with hypostome; at maturity the distal chamber globular or flattened, tentacles of blastostyle not reduced, or partly atrophied.

Nematocysts of two kinds present on hydranth, none on gonophores:

- small microbasie euryteles, capsule pyriform, $7 \times 3 \mu\text{m}$, shaft $5 \mu\text{m}$ long, thread fine (Fig. 77). Abundant on tentacles.
- large (?) macrobasie euryteles, capsule paddle-shaped, $28-30 \times 11-14 \mu\text{m}$, shaft very long and thick, length-width ratio 2.9:1, heavily armed with overlapping leaf-like spines, undischarged thread lying in a loose loop inside capsule (Figs 78, 79). Abundant around hypostome.

MEASUREMENTS, mm: *Stem* and *branches*, max. width, 0.18, *Branch*, proximal width, 0.075-0.13; *Pedice*l, (or branch) length, 1.0-2.0, distal width, 0.1-0.13; *Hydranth* (preserved material) width below tentacles, 0.4-0.5; *Male gonophore*, length, 0.33-0.38, diameter of distal chamber, 0.25.

COLOUR: Perisarc pale honey brown, colour of living hydranths unknown.

REMARKS: The cnidome of *E. aylingae* resembles that of another tropical species, *E. infundibuliforme* Kirkpatrick, 1890, in the presence of large macrobasic euryteles around the hypostome. However, these nematocysts differ from those of *E. infundibuliforme* in both the shape of the capsule and morphology of the shaft. Those of *E. aylingae* possess a very long, distally-swollen shaft; no threads were observed. In the few fully-discharged specimens available for study, the entire length of the shaft is covered by overlapping leaf-shaped spines. These spines point forward in the undischarged state, then reverse to the normal backward-facing direction upon complete discharge. The nematocysts are remarkably like those figured and described by Kirkpatrick (1890) from *Cladocoryne haddoni* from Torres Strait. Although the type material is meagre, I have no hesitation in regarding this as a new species, clearly identifiable by the unusual cnidome.

The material from Perth, Western Australia, comprises a small, sparingly-fertile male colony with 2-chambered gonophores. Although the stems are small and straggling, similar to the holotype, the colony itself is somewhat more robust. The Bass Strait specimen comprises only a single hydranth with male gonophore buds. While the material of both specimens is inadequate for firm identification, the cnidome of each is sufficiently like that of *E. aylingae* for them to be provisionally referred to this species. Although undischarged in both Western Australian and Bass Strait specimens, the hypostomal nematocysts are clearly macrobasic euryteles, the typically heavily-armed shaft lying in a loose coil along the walls of the capsule. The thread appears to be very long and fine. Dimensions of the nematocysts of both the Western Australian and Bass Strait specimens are given for comparison.

The Bass Strait record is the deepest record of *Eudendrium* from the Australian coastline.

MEASUREMENTS, μ m:

	Tentacular microbasic euryteles		Hypostomal macrobasic euryteles
	capsule	shaft	
Bass Strait	9	—	27-30
(MVF50722)	\times 3-3.5		\times 9-10 L/W ratio, 2.8
W.Australia	8-9		35-36
(MVF50723)	\times 3-4	7 \times 2	\times 13-15 L/W ratio, 2.8

ETYMOLOGY: The species is named for Avril Ayling, who collected the type material on the Great Barrier Reef, Queensland.

Eudendrium currumbense n. sp.

Figs 80-83

Eudendrium capillare Alder, 1856. Pennycuik, 1959: 168 (in part).

Pennycuik (1959, p. 168) provisionally assigned her material from Currumbin, Queensland, to *E. capillare* Alder, 1856, rather than to the superficially similar *E. generale* von Lendenfeld, 1885. Her identification rested partly on unreliable morphological features such as height and branching of the colony. Examination of the cnidome of Pennycuik's material shows it to be neither of these species. It is here regarded as a new species, described below.

TYPE MATERIAL AND RECORDS: Holotype, QMG5510, one sterile colony, alcohol preserved, on sponge in rock pool, Currumbin, Queensland, 28° 16' S, 153° 26' E; coll: P. Pennycuik, 1/7/51.

OTHER MATERIAL: One sterile colony on weed, 5 km NE of Bundaberg Light, Queensland, 24° 52' S, 152° 48' E, Agassiz trawl; coll: M. Blackburn, 14/9/38.

DESCRIPTION OF HOLOTYPE: Colony sterile, comprising several stems growing through the sponge tissue. Stems up to 6 mm in height, unfasciated, slender, irregularly branched, branches twisted and bent, a few indefinite annulations at origin and at intervals along the branch and sometimes below the hydranth. Hydranths small, with 20-24 tentacles.

Nematocysts of two kinds present:

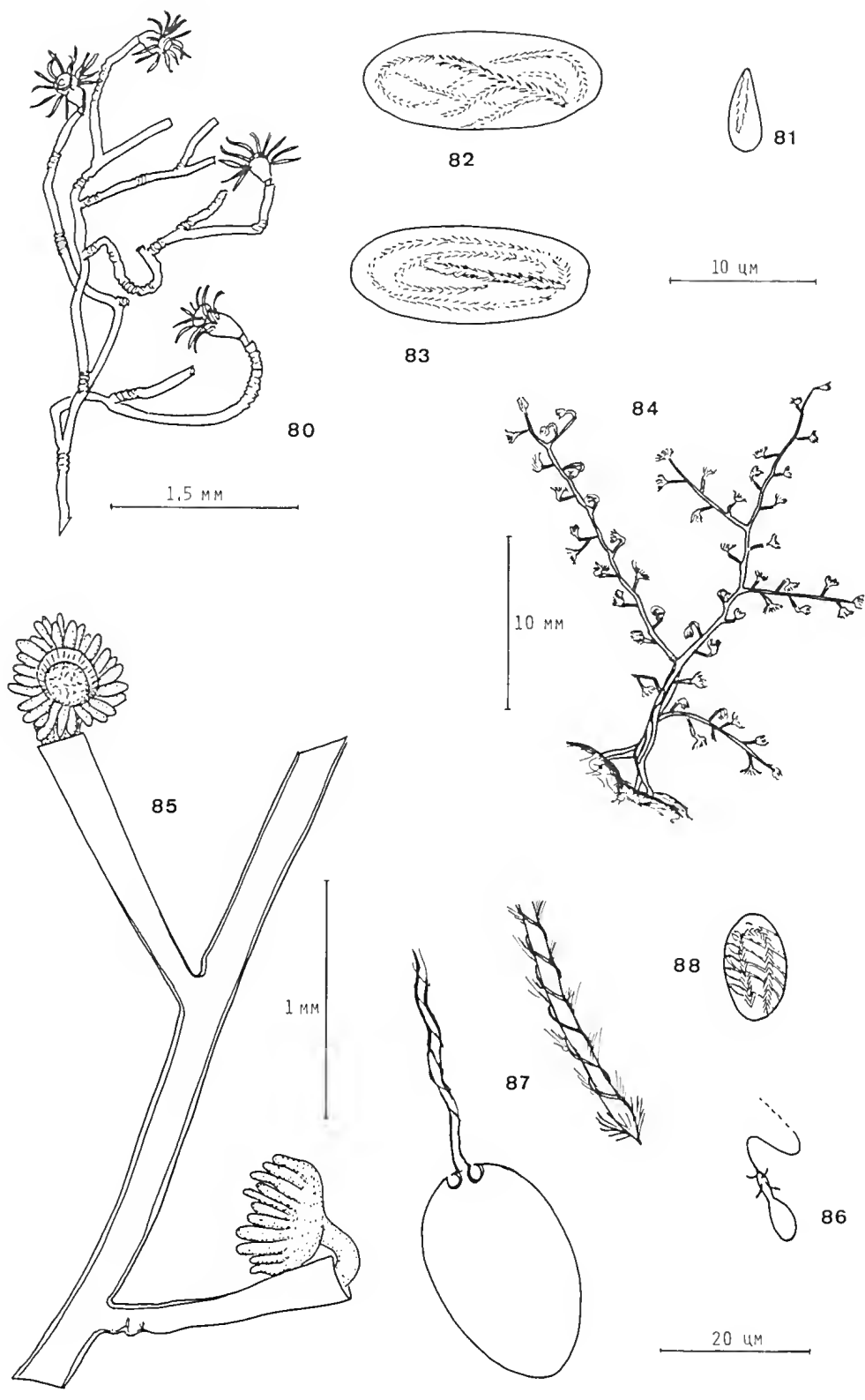
- small microbasic euryteles, capsule pyriform, 6 \times 2.5-3 μ m, none discharged, undischarged shaft lying slightly oblique to long axis of capsule (Fig. 81). Abundant in tentacles.
- (?)macrobasic euryteles, 16-19 \times 6-8 μ m, length-width ratio 2.5:1, shaft not well preserved in those discharged, undischarged shaft lying in 4-5 loose figure of eight coils in capsule or in coils parallel to capsule walls, depending upon the angle of view (Figs 82, 83). A few scattered on hydranth and on the hypostome.

MEASUREMENTS, mm, [including those of Pennycuik (1959)]; *Pedice*l, width below hydranth, 0.09-0.12; *Hydranth* (preserved material), length, base to hypostome, 0.23-0.54, width below tentacles, 0.15-0.25, width across extended tentacles, 0.17-0.33, length of tentacles, 0.23-0.46.

COLOUR: Proximal stems honey brown, becoming paler distally. Colour of living hydranth unknown.

REMARKS: In the collection of the Queensland Museum there is a small, very poorly-preserved colony of *Eudendrium* from Bundaberg, Queensland. The cnidome of this specimen shows it probably to be *E. currumbense*. While the sterile colony of *E. currumbense* is virtually indistinguishable from other small species such as *E. capillare*, *E. nambuccense* and *E. pennycuikae*, the presence of heteronemes in the cnidome readily separates it from these species.

ETYMOLOGY: The species name refers to the type locality.



Eudendrium infundibuliforme Kirkpatrick, 1890

Figs 84-88

Eudendrium infundibuliforme Kirkpatrick, 1890; 606, Pl. 14, Fig. 3. Pennycuik, 1959: 167. Rösler, 1978: 96, Pl. 17, Figs 3-5.

MATERIAL AND RECORDS: Holotype, BM1890.7.23.3, Stn 2, 10 m deep, 32 km NNW of Warrior Island, Torres Strait (Kirkpatrick). MVF50501 sterile colony, formalin preserved, Basilisk Passage, depth 10 m, Port Moresby, Papua New Guinea, 9° 30' S, 147° 10' E; coll: J. E. Watson (SCUBA), November, 1979. MVF50502, male colony, formalin preserved, Carter Reef, Queensland 14° 32' S, 145° 35' E; depth, 15 m; coll: A. L. Ayling (SCUBA), 16/3/83. MVF50528, sterile colony, formalin preserved, Great Detached Reef, Queensland 11° 58' S, 143° 58' E; coll: A. L. Ayling (SCUBA) (no depth), 22/5/79.

DESCRIPTION: It has not been necessary to examine the type material of *E. infundibuliforme* since this is one of the few Australian species easily identifiable on colony characters alone. The following description supplements that of Kirkpatrick. The present specimens are erect, arborescent colonies from 3-8 cm in height. The main stems are straight, or gnarled and twisted, strongly fascicled, arising from a thick rootstock, the fascicular tubes running halfway up the main stem and along the proximal region of the main branches. Branching sparse, more or less in one plane, irregularly alternate, some secondary branching present. Perisarc of main stems indistinctly ringed at intervals, branches with 3-4 proximal annulations, perisarc otherwise smooth and shining.

Hydranth pedicels regularly alternate, with 2-5 obscure proximal annulations, or wrinkled throughout. Hydranths large, with up to 30 tentacles and a wide hypostome (preserved material). The male specimen from Carter Reef is sparingly fertile, gonophores 2 or 3-chambered, one or two borne on a fully-developed hydranth with hypostome. Immature distal chamber slightly elongate with a distinct apical peak, lost at maturity; mature chamber bead-shaped.

Nematocysts of two kinds present in all specimens:

- small microbasic euryteles, capsule $6 \times 3 \mu\text{m}$, shaft $5 \mu\text{m}$ long, with a few prominent spines (Fig. 86). Abundant in tentacles.
- very large holotrichous macrobasic euryteles, capsule egg-shaped, $30-34 \times 18-22 \mu\text{m}$; shaft $400 \mu\text{m}$ long, slightly expanded at tip, armed with spirals of bristles over entire length and with additional

larger bristles in the distal region (Fig. 87). Abundant around hypostome.

A third kind of nematocyst is present, although rare, in all specimens except those from Carter Reef. These are small ?macrobasic euryteles, capsule egg-shaped, $12 \times 8 \mu\text{m}$, (none discharged), site on hydranth unknown (Fig. 88).

MEASUREMENTS, mm: *Stem*, proximal width, 0.6-2.25; *Branch*, proximal width, 0.1-0.35; *Pedicel*, proximal width, 0.08-0.15, distal width, 0.18-0.33, length, 0.8-1.63; *Hydranth*, (preserved material), width below tentacles, 0.38-0.7; *Male gonophore*, diameter of distal chamber, 0.2.

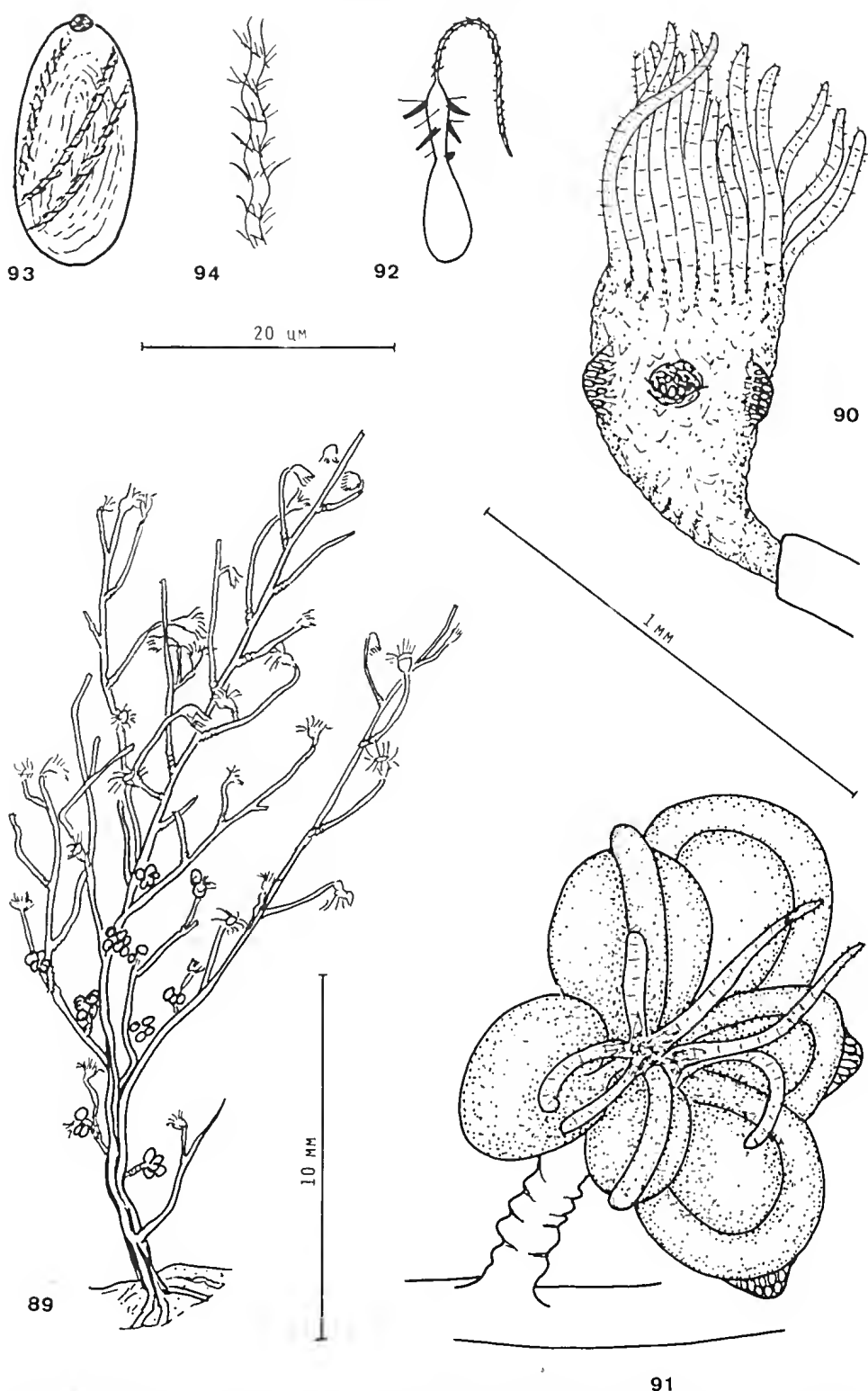
COLOUR: Older stems deep brown, grading to lighter brown on younger parts. Living hydranths deep yellow. **REMARKS:** *Eudendrium infundibuliforme* is an easily recognisable species by its robust, arborescent habit, distally-expanding, hydranth pedicels, and especially by the cnidome. Kirkpatrick (1890) remarked upon the "large peduncular portion between the end of the perisarc and the base of the tentacles". Elongation of the hydranth is usually a chance artefact of preservation in most species of *Eudendrium* and is therefore regarded as being of little diagnostic value. It is, however, such a very constant feature in both living and preserved specimens of *E. infundibuliforme* that it can justifiably be regarded as being characteristic of the species.

Rösler (1978) doubted the validity of Kirkpatrick's reference of the Torres Strait specimens to *Eudendrium* on the assumption that a distally-widening, hydrothecal pedicel is neither typical of the genus, nor even of the Athecata. This shape of pedicel is not, however, unique among the Athecata, since it is also present in the genus *Merona* (F. Clavidae) (see Watson 1978). Moreover, the abundant material of *E. infundibuliforme* available to the present study demonstrates conclusively through colony morphology, reproductive structures and the cnidome that this hydroid is clearly a species of *Eudendrium*.

As Kirkpatrick's material was sterile, the Queensland specimen provides the first record of the reproductive structures of the species. Unfortunately, the sparingly fertile material is inadequate to determine whether the few male gonophores borne below the hydranth are a number normal for the species. The very large hypostomal nematocysts are a distinctive feature. Although I have been unable to isolate a thread for examination, these nematocysts are considered, following Werner (1965), to be holotrichous macrobasic euryteles. The third, rare nematocyst present in the majority of

Figs 80-83—*Eudendrium currumbense* n. sp. Drawn from holotype, Currumbin, Qd. 80, Stem. 81-83, Nematocysts, drawn to same scale. 81, Microbasic eurytele from tentacles, undischarged. 82, 83, Undischarged macrobasic euryteles from hydranth, viewed from two aspects. 82, showing apparently obliquely-coiled shaft. 83, showing apparently spirally-coiled shaft.

Figs 84-88—*Eudendrium infundibuliforme* Kirkpatrick, 1890. 84, Colony from Carter Reef, Qd. 85, Part of branch from specimen from Port Moresby, Papua New Guinea. 86-88, Nematocysts, drawn to same scale. 86, Microbasic eurytele from tentacles, discharged. 87, Large macrobasic eurytele from hypostome, proximal and distal regions of shaft shown. 88, Smaller ?macrobasic eurytele, undischarged, in specimen from Port Moresby.



Figs 89-94—*Eudendrium glomeratum* Picard, 1951. Specimen from Cape Jaubert, W.A., assigned by Jäderholm (1916) to *E. pusillum* von Lendenfeld, 1885. 89, Whole colony. 90, Hydranth, showing button-shaped nematocyst pads. 91, Female blastostyle with gonophores at several stages of maturity; nematocyst pads on spadix of young gonophores. 92-94, Nematocysts, drawn to same scale. 92, Microbasic eurytele from tentacles. 93, ?Macrobasic eurytele, undischarged, from nematocyst pad on hydranth. 94, part of discharged shaft of ?macrobasic eurytele showing spirals of fine bristles.

specimens is very similar to the larger macrobasic euryteles of the hypostome.

DISTRIBUTION: *Eudendrium infundibuliforme* has been previously known only from the type locality in Torres Strait. The present records extend its known range further north to Papua New Guinea and south along the Great Barrier Reef. It may eventually prove to be a common hydroid of deeper tropical waters.

Eudendrium glomeratum Picard, 1951

Figs 89-94

Eudendrium glomeratum Picard, 1951: 338; 1955: 183.

Rossi, 1961: 73. Teissier, 1965: 14. Fey, 1969: 391.

Rösler, 1978: 88, Pl. 14, Fig. 6.

Eudendrium pusillum von Lendenfeld, 1885: 352.

Thornely, 1904: 110, Pl. 1, Fig. 5. Jäderholm, 1916: 3.

?*Eudendrium indopacificum* Stechow, 1923: 59.

Eudendrium ramosum (Linnaeus, 1758). Motz-Kossowska, 1905: 54, Pl. 3, Fig. 16.

MATERIAL AND RECORD: Swedish Museum of Natural History No. 498, one female colony, alcohol preserved, 72 km WSW of Cape Jaubert, Western Australia, 18° 56' S, 121° 39' E, depth 99 m; coll: Swedish Scientific Expedition to Australia 1910-1913, 6/7/11.

Thornely (1904) referred a specimen from the Gulf of Manaar, Sri Lanka, to *Eudendrium pusillum* von Lendenfeld, 1885. On the basis of its resemblance to Thornely's figure, Jäderholm (1916) also referred a specimen from Cape Jaubert, north-western Australia, to *E. pusillum*. Briggs (1922) expressed the opinion that Thornely's specimen was not *E. pusillum* although he did not propose a new name. At the same time he substituted the name *E. lendenfeldi* for *E. pusillum* on the grounds of pre-occupation of the latter name. Stechow (1923) then proposed a new name, *E. indopacificum*, for Thornely's and Jäderholm's specimens, apparently without examination of their material.

I have been unable to trace Thornely's specimen and agree with Rösler (1978), that it must be presumed lost. Through courtesy of the Swedish Museum of Natural History I have been able to examine Jäderholm's specimen and compare it with a female colony of *E. glomeratum* Picard, 1951 from the Gulf of Genova, loaned by the British Museum (Natural History). The specimens are virtually identical in colony morphology and in characters of the cnidome. Only a few nematocysts in the Australian material are discharged and these are in poor condition; the supplementary nematocysts of the cnidome appear to be macrobasic euryteles which, in size and coiling of the shaft, agree closely with those of *E. glomeratum*. Although Picard (1951) describes the nematocysts of *E. glomeratum* as being arranged in projecting buttons around the lower hydranth body, the specimen from the Gulf of Genova displays a number of configurations varying from an uninterrupted nematocyst ring around the hydranth to discrete groups arranged in a digitate pattern scattered around the body of the hydranth.

Rösler (1978) mentions the similarity of both form and cnidome of *E. glomeratum* and *E. ramosum*. This has, apparently, led to misidentification in the past, since recent critical re-examination of the holdings of *E. ramosum* in the British Museum (Natural History) has revealed some specimens from England and Ireland to be *E. glomeratum* (Cornelius & Boero pers. comm.). The two species from Australia as known at present are, however, easily differentiated by colony form, *E. glomeratum* being arborescent while colonies of *E. ramosum* are straggling, although robust in habit. The following redescription of *E. glomeratum* from Australia includes that of Jäderholm (1916).

DESCRIPTION: The specimen is a mature female colony 30 mm in height comprising a single stem growing from a rootstock embedded in sponge. The main stem is almost straight and the lower third is lightly fasciated. With one exception, the branches are unfasciated. The branches are given off from around the main stem in roughly three planes, upwardly directed, rebranching common, 3-6 annulations at origin, perisarc smooth and shining throughout. Hydranths terminal on branches, moderately large, with 24-28 tentacles, body of 50% of the hydranths with 3-5 prominent button-shaped nematocyst pads in the proximal region. Female gonophores in various stages of maturity are borne in a cluster of 4-6 on the body of the hydranth, spadix of immature gonophore unbranched, with a distal nematocyst pad, lost at maturity. Mature blastostyle with either a normal number of tentacles or a reduced number of 6-8 partly-atrophied tentacles as described by Jäderholm. Mature gonophore elongate, enclosed in a thin pellicle, retained in original position on hydranth or slightly displaced down the blastostyle.

Nematocysts of two kinds present:

- microbasic euryteles, 7-8 × 3-4 μm, shaft 4-6 μm long, broad, with prominent spines and bristles, thread ropy (Fig. 92). Abundant in tentacles. Length-width ratio, 2:1.
- large (?) macrobasic euryteles, capsule bean-shaped, ends blunt, 19-22 × 9-10 μm, few discharged, length-width ratio 2.3:1. Distal part of shaft thick and armed with bristles, undischarged shaft lying in one or two loosely oblique coils inside capsule (Fig. 93). Very abundant in the nematocyst pads on hydranths and on the gonophores.

MEASUREMENTS, (mm): *Stem*, proximal width, 0.1; *Branches*, max. length, 7.4, width at origin, 0.13-0.18, width below hydranth, 0.13-0.18; *Pedicel*, length, 1.5-3.0; *Hydranth* (preserved material), width below tentacles, 0.23-0.38; *Gonophores*, width of cluster, 0.75-0.95, length of mature gonophore, 0.3-0.38.

DISTRIBUTION: Mediterranean Sea (Picard 1951), north-western France (Teissier 1965, Fey 1969) England, Ireland (Cornelius & Boero pers. comm.) and north-western Australia.

DISTRIBUTION AND ECOLOGY

DISTRIBUTION: The genus *Eudendrium* is now recorded from about half of the Australian coastline, encompassing the tropical waters of the Great Barrier Reef and Torres Strait from 11° S to cool temperate Bass Strait at 38° S and the Pacific coast in the east to the Indian Ocean in Western Australia (Fig. 95). There are, however, large gaps in the record, namely those of the northern coastline and Timor Sea, the shores of the east Indian Ocean in Western Australia, the Great Australian Bight and the Tasmanian region. The sparseness of the record from most of these regions probably reflects the difficulty of access and lack of collecting intensity rather than any impoverishment of the *Eudendrium* fauna. The absence of records from the Great Australian Bight, particularly the eastern Bight in South Australia, and from Tasmania, is, however, noteworthy, since localities in these regions have been intensively collected by the author and others on several occasions. The patchiness of the record in some of these

areas may therefore be partly attributable to distributional patterns, indicating some avoidance by *Eudendrium* of clearer oceanic waters. Avoidance of high light intensity by *E. ramosum* on the coral reefs of the West Indies and the Red Sea has been pointed out by Mergner (1972, 1977).

The zoogeographic record (Table 1) suggests a relatively endemic *Eudendrium* fauna, there being only one out of the seventeen species recorded, *E. aylingae*, occurring in three biogeographic provinces, the tropical Solanderian, subtropical Damperian and cool temperate Flindersian. The Flindersian record is, however, somewhat doubtful owing to paucity of material. Although it might be expected that the cosmopolitan *E. capillare* should occur through all Australian biogeographic provinces, the only reasonably certain record so far is from the temperate Peronian together with a doubtful record from the Solanderian. Although probably world-wide in distribution, *E. capillare*, as shown for Australian material in this study, has in the past been confused with other species. There is a great

TABLE 1 DISTRIBUTION OF *Eudendrium* SPECIES RECORDED FROM AUSTRALIA

Species	SOLAN- DERIAN									Other Regions
	N. Great Barrier Reef	Southern Queensland	N. New South Wales	Central New South Wales	S. New South Wales	Eastern Bass Strait	Central Bass Strait	South W. Australia	Central W. Australia	
1. <i>E. minutum</i>							p			
2. <i>E. pennycuikae</i>		p								
3. <i>E. nambucense</i>			p				p			
4. <i>E. capillare</i>	?p			p						Cosmopolitan
5. <i>E. terranova</i>							p			Northern New Zealand
6. <i>E. corrugatum</i>		p								
7. <i>E. ramosum</i>		p					p			Britain, North Atlantic, Mediterranean, Seychelles, South Africa.
8. <i>E. kirkpatricki</i>	p								p	Papua New Guinea.
9. <i>E. generale</i>				p		p	p			?South China Sea.
10. <i>E. merulum</i>	p					p				
11. <i>E. carneum</i>								p		N and S America, Bermuda, St. Helena, South Africa.
12. <i>E. racemosum</i>	p	p								Mediterranean, South China Sea, Japan, Seychelles.
13. <i>E. balei</i>				p	p	p	p			
14. <i>E. aylingae</i>	p						p	p		
15. <i>E. currumbense</i>		p								
16. <i>E. infundibuliforme</i>	p									
17. <i>E. glomeratum</i>									p	Papua New Guinea. Mediterranean, north- western France, England, Ireland.

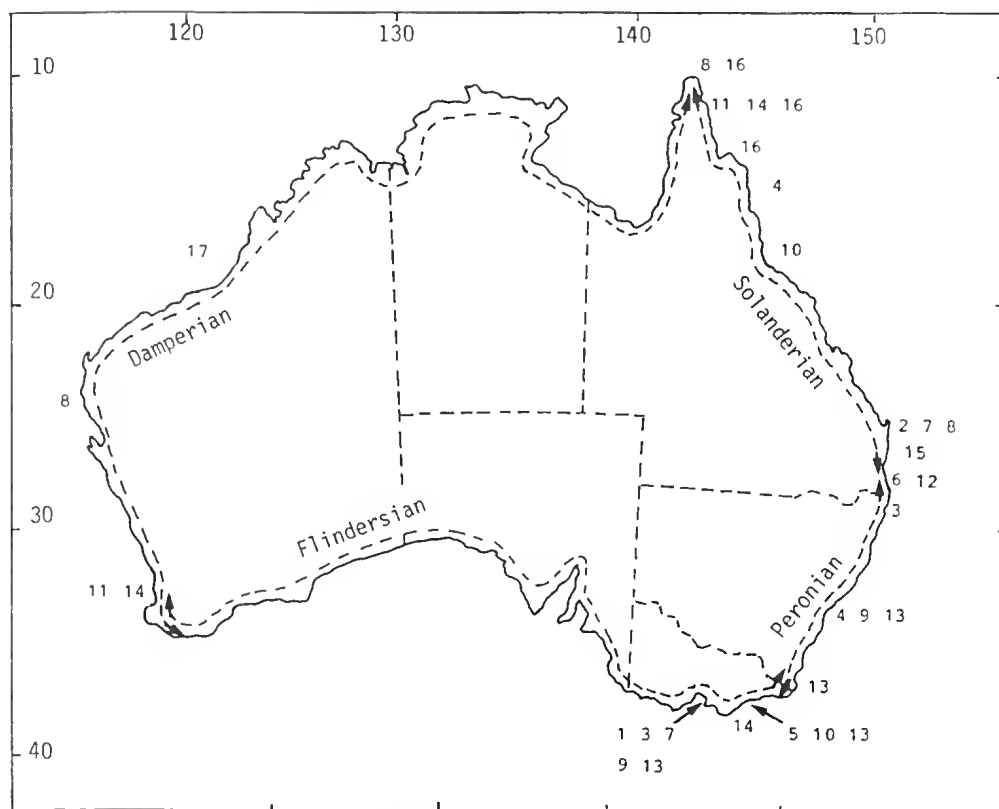


Fig. 95—Distribution of the *Eudendrium* fauna of Australia. Map shows coastal biogeographic provinces. Numbers refer to species listed in key order.

need for a critical world revision to place this species, as well as many other species of *Eudendrium*, in their proper systematic and distribution contexts.

Eight species are recorded from two Australian provinces and eight from only one province. Those recorded from adjacent provinces are *E. nambuccense*, *E. generale* and *E. balei*, all of which range from the warm temperate northern extreme of the Peronian to the Flindersian province of the east coast (Fig. 95). Two species, *E. ramosum* and *E. merulum*, are so far recorded from two widely-separated provinces without records from the intervening regions. *Eudendrium ramosum* is recorded near the boundary of the Solanderian and Peronian in southern Queensland, its range also extending south into Bass Strait, while *E. merulum* is recorded from the northern Great Barrier Reef and eastern Bass Strait. Although widely separated by some 3,500 km of coastline, the biogeographic distance between records of *E. kirkpatricki* is not significant, since summer water temperatures in Shark Bay in the Damperian province of Western Australia approach those of the tropical Great Barrier Reef.

Of the eight species recorded from one province only, three, *E. pennycuikae*, *E. corrugatum*, and *E. curumbense*, occur near the Solanderian-Peronian boundary in southern Queensland. There are no records of species endemic to the Peronian, while two species, *E.*

minutum and *E. terranova*, are recorded only from the cooler Flindersian of Bass Strait.

The present biogeographic record suggests a highly endemic Australian *Eudendrium* fauna. Of the seventeen species recorded here, only five (29%), are known from outside the Australian region. Of these, *E. capillare* is cosmopolitan, *E. carneum* ranges from the east coast of South America (Vannucci 1954, Wedler 1975), the Caribbean (Vervoort 1968), the Atlantic coast of North America (Clarke 1882), to parts of the southern hemisphere including the east coast of South Africa (Millard 1975). *Eudendrium racemosum* is known from the Mediterranean Sea (Mergner 1957), the South China Sea (Leloup 1937), the north-western Pacific (Hirohito 1969), and the western Indian Ocean (Millard & Bouillon 1973); *E. ramosum* is widely distributed in the North Atlantic, although some of the records are doubtful (Millard 1975), the Mediterranean Sea (Picard 1955), the Red Sea (Mergner 1977), the western Indian Ocean (Millard 1975) and the West Indies (Mergner 1975); *E. glomeratum* has been recorded from the Mediterranean Sea (Picard 1951), north-western France (Teissier 1965, Fey 1969), and recently, the coast of England and Ireland (Cornelius & Boero pers. comm.).

The range of two species, *E. kirkpatricki* and *E. infundibuliforme*, is now extended northward to Papua

New Guinea. *Eudendrium terranova* is the only species recorded in this study common to Australia and New Zealand. This is surprising, considering the overall similarity of the trans-Tasman thecate hydroid fauna. Future collecting around New Zealand might reveal more species common to both regions.

The only record of an Australian species from outside the Australian region is that of *E. generale* var. *amoyicum* from the South China Sea (Hargitt 1927, Ling 1938). However, this record is here considered doubtful and needs verification from examination of fresh material (p.200).

The *Eudendrium* fauna of the seas surrounding the Australian region is so poorly known, and in many instances the taxonomy so unreliable, that there is little value in making regional biogeographical comparisons. South Africa is the only adjacent southern hemisphere region for which there is any useful information. Millard (1975) recognised eight species from southern Africa, only two of which, *E. capillare* and *E. carneum*, are so far known to occur in Australia. Stepanjants (1979) recognised three species from the Antarctic, but only the circumpolar *E. antarcticum* Stechow, 1921, occurs in the region south of Australia. This species has not, however, been recorded in the present study.

The record suggests that *Eudendrium* may be a shelf genus in Australia, inhabiting relatively shallow waters ranging from the intertidal zone (*E. curumbense*) to depths of 70 m (*E. aylingae*) and 99 m (*E. glomeratum*). The shallow bathymetric ranges recorded for most of the species is undoubtedly an artefact of the depths readily accessible to small dredges and SCUBA, by which means the major part of the present collection was made. The record may thus not reflect any marked preference of the genus for the continental shelf. Nonetheless, world-wide, deep-water records of *Eudendrium* are comparatively rare, some of the deepest being: *E. antarcticum* Stechow, 1921, from 650 m in the Kerguelen Islands (Millard 1977); *E. rameum* Pallas, 1766 from 191 m, also in the Kerguelens (Allman 1888); *E. rameum* from 310 m off the Hawaiian Islands (Nutting 1905); and *E. deciduum* and *E. ramosum* from 174 m and 220 m respectively in the Red Sea (Mergner & Wedler 1977). The deepest record of any species of *Eudendrium* is that of 1,267 m off Newfoundland (Pictet & Bedot 1900).

Ecology: Field observations by the author and others indicate choice of a rather narrow range of habitat by many species of *Eudendrium*. Most of the species collected by the author in this study have been found in habitat of low light intensity, such as shaded or cryptic situations, similar to preferences of *Eudendrium* reported by Wedler (1975), Mergner (1977), and Mergner and Wedler (1977). Colonies of some species, for example, *E. balei* and *E. generale*, exhibit their most luxuriant development over a narrow band of irradiance, suggesting that light intensity may be a controlling factor in their distribution with depth. The observations of Light (1913) on the presence of zooxanthellae in the hydranth of *E. griffini* (= *Myrionema*

griffini) is of interest in this regard, suggesting that bathymetric distribution and choice of habitat by *Eudendrium* may be dictated to some extent by symbiotic relationships.

Underwater observations by the author show that the Australian species of *Eudendrium* avoid turbulent water movement such as breaking waves, which are likely to destroy the unprotected hydranths. Stolonal colonies with straggling, unfascicled stems or only lightly-fascicled stems, for example, *E. generale*, *E. ramosum* and *E. merulum*, occur in places where oscillatory water movement such as "edge effects" (Foster 1975) are dominant. The flexibility of these colonies probably allows utilisation of habitats that would be too rigorous for species with more rigid stems. The most luxuriant colonies of robust, bushy species such as *E. balei* and *E. ramosum*, seen by the author, occur in the swift-flowing, tide-channels of Western Port and at Port Phillip Heads, Victoria. The large size attained by these colonies is probably a reflection of the abundant food supply borne on currents which often exceed 200 cm sec⁻¹. Preference of two species, *E. racemosum* and *E. carneum*, for reef habitat with good current flow has been noted by Wedler (1975), Mergner (1977) and Mergner and Wedler (1977). These species have also been found occupying similar habitats in the present study.

Taller, arborescent colonies, such as *E. terranova* and *E. infundibuliforme*, which have stiff, fascicled stems, seldom occur in open situations, preferring the sheltered habitat of small caverns and overhangs in relatively shallow ocean water. In these situations, an arborescent or fan-shaped colony forms a web which can be oriented more or less normal to the micro-patterns of water movement, thus maximising efficiency in capture of food.

Observations on the species of *Eudendrium* in Australia do not indicate that they display any marked preference for particular substrates. Most are epizootic, occurring on sponges, compound ascidians, bryozoans, brachiopods and bivalves, and sometimes on other cnidarians. Under favourable conditions, some of the smaller species, for example, *E. merulum*, *E. capillare* and *E. generale*, may form dense hydroid meadows on the substrate. Stolonal species sometimes occur as epiphytes on marine plants, for example, *E. pennycuikae* on the seagrass *Halophila spinulosa*; *E. capillare* on the brown alga *Hormosira banksii*; and, simple stems of *E. terranova* on the green alga *Caulerpa flexilis*.

The strongly colonial habit of many species may well be a consequence of rapid settlement of the short-lived planula larva near the parent colony (Wasserthal & Wasserthal 1973). Gregarious settlement during the short larval stage also occurs in this manner among certain nemertean (Hughes 1977) and tubularian hydroids (Watson 1980). It has the advantage of strengthening the colony through addition of numerous fascicular tubes as well as giving protection to young hydranths immersed among the stems of the colony. These settle-

ment patterns are probably the reason for the downwardly-growing fascicular tubes characteristic of the large colonies of *E. carneum* observed at Fremantle, Western Australia.

Some information is available on the life cycle of certain species of *Eudendrium* (Vannucci 1954, Vervoort 1946, Wasserthal & Wasserthal 1973), but little is known about the longevity of individual colonies other than observations of *E. carneum* by Wedler (1975). Underwater observations on *E. balei* at Crawfish Rock, Western Port, Victoria, have shown that some colonies have occupied the same place for at least five years (pers. obs.). Growth commences from the moribund hydrorhizal filaments embedded in compound ascidian or sponge in late winter to spring. The colonies become reproductive during higher water temperatures over the summer months then die off as temperatures drop with the approach of winter. Longevity seems to be determined more by the stability and longevity of the substrate species rather than by ageing of the hydroid colony itself.

With large hydranths and exposed, yolk-rich ova (Mergner 1974), colonies of *Eudendrium* are highly vulnerable to predation. Observations in this study have shown that some species of *Eudendrium* are heavily preyed upon by pycnogonids and nudibranchs, and some are occasionally grazed by small fish. Pycnogonid larvae at the protonymphon stage have been observed in laboratory studies, feeding upon *E. ramosum* from Port Phillip Heads. Adults of *Nymphon aquidigitatum* Haswell have also been observed in Western Port over the summer months, feeding upon colonies of *E. balei*.

Associations of nudibranchs with *Eudendrium* are also of very common occurrence in southern Australian waters. Hydranths and ova of most of the species of *Eudendrium* collected by the author, are grazed by small, brightly-coloured aeolid nudibranchs, mainly of the genera *Flabellina* and *Coryphella*, as well as by *Doto ostenta* Burn. The nudibranchs may spend some, or all, of their life cycles on the hydroid colonies, grazing the hydranths and gonophores and laying egg ribbons among the branches. Often, it is possible to provisionally determine the hydroid host species from examination of the nematocysts retained in the cerrata of the aeolid.

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A NEW LATE DEVONIAN ACANTHODIAN FISH FROM MT. HOWITT, VICTORIA, AUSTRALIA, WITH REMARKS ON ACANTHODIAN BIOGEOGRAPHY

By J. A. LONG

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ABSTRACT: A new acanthodiform acanthodian, *Howittacanthus kentoni* gen. et sp. nov., is described from the Frasnian lacustrine Mt. Howitt site, eastern Victoria. *Howittacanthus* is characterized by: a palaeoquadrate ossified in three divisions with both otic and auxiliary otic cotyli in contact with the braincase; autopalatine with posterior basal process; slender body form with small pelvic fins closer to anal than to pectoral fins; and all fin-spines ornamented with a single ridge. Ontogenetic data obtained from *Howittacanthus* agree with the findings of Zidek (1985) for *Acanthodes*. The family Acanthodidae is redefined. *Howittacanthus* is placed as the possible sister taxon to a group containing *Acanthodes* and *Acanthodopsis* by shared characters of the jaw cartilages. A Euramerican centre of origin is proposed for acanthodiforms, gyracanthids and diplacanthoids. These groups probably entered the East Gondwana Province following faunal interchange with the Euramerican Province sometime in the Middle Devonian.

Few acanthodian fishes are known from Australia, and the only articulated complete fish come from the Late Devonian Mt. Howitt site, the Lower Carboniferous Mansfield Basin (both in Victoria), and from the Givetian Bunga Beds of New South Wales. The Mansfield Basin fauna was described by Woodward (1906) as containing three acanthodians, *Gyracanthides murrayi*, *Acanthodes australis* and *Eupleurognmus creswelli*. *Eupleurognmus* was erected on parts of the trunk squamation which showed enlarged scales flanking the lateral line. Such scales are now known to also occur on *Acanthodes* (Zidek 1976) and the genus *Eupleurognmus* cannot be substantiated. Similarly *Acanthodes australis* was not defined by unique features, and, as it is only imperfectly known from the tail, it cannot be maintained as a separate species and should be referred to as *Acanthodes* sp. Articulated acanthodians from the Bunga Beds (Fergusson *et al.* 1979) possess two dorsal fins and apparently lack dermal shoulder girdle armour. They are provisionally identified as ischnacanthids but details of the head are not preserved and the presence of gnathal bones, which characterize the Ischnacanthida, cannot be demonstrated. The Mt. Howitt acanthodians show the best preservation; the fish are preserved in finely-laminated shale which enables all aspects of their skeletal morphology to be revealed by latex casts after the friable bone is dissolved in weak hydrochloric acid. The Mt. Howitt fauna contains one of the most diverse and well-preserved assemblages of freshwater Late Devonian fishes in the world, including several species of placoderms (Long 1982, 1983a, 1984), osteichthyans (Long 1985) and acanthodians. Aside from the new acanthodiform (here used in the sense of Order Acanthodida) described in this paper one other acanthodian has been described from the fauna, a deep-bodied diplacanthoid, *Culmacanthus stewarti* (Long 1983b). Elsewhere in Australia acanthodiforms are known only from a new occurrence in the Raymond Formation, Drummond Basin, Queensland. These specimens are three-dimensionally preserved isolated bones (including

basisphenoids, scapulocoracoids and jaws) belonging to a new genus. Current preparation of new blocks of the Raymond Formation bone-bed should produce much more of this important acanthodian material for description in the near future.

Although the acanthodiforms are known from the Early Devonian to the mid Permian, the structure of the group is known primarily from one genus, *Acanthodes* (Miles 1964, 1965, 1968, 1973a, 1973b). *Acanthodes*, the most successful member of the group, flourished worldwide during the Carboniferous and Permian periods, long after most other acanthodian groups had declined. Relationships of the acanthodians, and acanthodiforms in particular, have been recently discussed by Long (in press). The new genus from Mt. Howitt is of biogeographic importance in being the earliest record of an acanthodiform which is geographically distant from the Euramerican Province (*sensu* Young 1981). It is also the first Devonian acanthodiform described from the Southern Hemisphere, and as specimens are preserved in all stages of growth the material allows some comment on the ontogenetic development of acanthodians in general.

The material was collected by Prof. J. Warren and staff and students of the Zoology Dept., Monash University, over two field seasons in the early 1970s. It was prepared by immersion in weak hydrochloric acid so that latex casts of the cleaned moulds could be made. It is housed in the Museum of Victoria, Melbourne (NMV).

SYSTEMATIC PALAEONTOLOGY

Subclass ACANTHODII
Order ACANTHODIFORMES
Family ACANTHODIDAE

DIAGNOSIS: Acanthodiform acanthodians which have an elongated gill chamber with very small, thin branchiostegals that extend only halfway across the length of the gill chamber. Pelvic fins small relative to pectorals.

REMARKS: Miles (1966) distinguished this family from the two other acanthodid families (Mesacanthidae and Cheiracanthidae) by possession of six characters. As some of these are also found in mesacanthids or cheiracanthids (e.g. lack of intermediate fin-spines, pectoral fin-spine of great length relative to body length in *Cheiracanthus*; scales with unornamented flat crown in mesacanthids), I have amended the diagnosis to include only derived characters of acanthodids. In addition to these characters, acanthodids often have the following features: pelvic fin-spines situated closer to pectoral fin than to anal fin; procoracoid with two attachment areas to scapulocoracoid; all fin-spines with single rib ornamentation. The new genus is referred to this family by having very small, slender branchiostegal rays, and, in addition, has a single rib on each fin-spine.

Denison (1979) did not recognize Miles' (1966) division of the order Acanthodida into three families, instead preferring to retain all genera in one family, Acanthodidae, because of the lack of recognizable synapomorphies defining these families. Mesacanthids appear to lack characteristic specializations, and are currently defined (Miles 1966) on plesiomorphic acanthodian features (presence of intermediate fin-spines; well-developed branchiostegal rays etc.). Some cheiracanthids exhibit synapomorphies; these are discussed in the phylogenetic section of this paper. Mesacanthidae therefore cannot be maintained as a valid family but should be regarded as a plesiomorphic sister group to the two definable acanthodid families, Cheiracanthidae and Acanthodidae.

Howittacanthus gen. nov.

1976 acanthodiforms; Marsden, p. 122

1982 Acanthodiformes; Long, p. 63.

1983a acanthodiform acanthodians; Long, p. 298

1983b acanthodiforms; Long, p. 51.

1983c *Acanthodes*-like acanthodian; Long, p.23, fig. 9.

1984 cf. *Acanthodes* sp.; Long & Turner, p. 240.

ETYMOLOGY: After Mt. Howitt where the specimens were found, and the Greek "acanthos", spine.

DIAGNOSIS: Slender acanthodid acanthodian reaching a maximum length of about 25 cm. Pelvic fin-spines half as long as the pectoral fin-spines and situated closer to the anal fin than to the pectoral fin. External length of dorsal fin-spine shorter than anal fin-spine, and all spines ornamented with one thick rib. Meckelian bone ossified as a single unit; palatoquadrate ossified as three divisions with otic and auxiliary otic cotyli present. Autopalatine with basal process in posterior half. Scapular short without suprascapular ossification. Procoracoid small and slender. Scales without ornament on the crown.

TYPE SPECIES: *Howittacanthus kentoni* sp. nov.

REMARKS: This acanthodid is distinguished from all others except *Acanthodes* and *Acanthodopsis* by having

the dual otic cotyli on the palatoquadrate, and *Acanthodopsis* is readily distinguished by the presence of teeth on the jaws (see Long in press, for a discussion of the systematic position of this genus). *Howittacanthus* is distinguished from *Acanthodes*, *Pseudacanthodes* and *Traquairichthys* by the placement of the pelvic fin closer to the anal fin (and by its absence in *Traquairichthys*). *Howittacanthus* closely resembles *Protogonacanthus* by its body shape and fin placement but differs in having singularly-ribbed fin-spines. Although *Carycinacanthus* is poorly known, it can be distinguished from *Howittacanthus* by the shape of the tail and ratio of anal fin-spine to dorsal fin-spine length.

Howittacanthus kentoni sp. nov.

Figs 1-6, 7A, 8, 9, 10E.

ETYMOLOGY: In honour of Prof. K. S. W. Campbell, Geology Dept., Australian National University for his contribution to the study of early vertebrates.

DIAGNOSIS: as for genus, only species.

MATERIAL: Holotype, NMV P179580, a complete individual (Figs 1A, 2). Paratypes, NMV P179582 (Figs. 1B, 4B, 5C) and NMV P179591 (Fig. 3E), showing details of the head. NMV P179570-P179629, individuals in various stages of growth.

LOCALITY AND AGE: Mt. Howitt Spur quarry, lower part of the Avon River Group (Long 1983a, Fig. 1). Late Devonian (Frasnian).

DESCRIPTION: *Howittacanthus* is a medium-sized acanthodid with a fusiform shape as in other genera. The head occupies one-sixth of the total length of the fish and the body had a depth/length index (x100) close to 13 in mature individuals. Proportions of fin-spine lengths to body lengths are shown in Table 1.

The head contained internally ossified jaw cartilages and gill rakers, and dermal sclerotic ring bones. The dorsal surface of the head was covered with small tesserae (tss, Fig. 4B) which are slightly larger than surrounding scales. On one large specimen, NMV P179598 (Figs. 3F, G, 4C, D), the lateral face of the dorsal ossification of the braincase is preserved, and therefore, the absence of the braincase in smaller specimens presumably indicates that it was only fully ossified in large individuals. All other skeletal elements in the head were presumably cartilaginous (gill arch bones and possibly endocranial components). The lateral face and part of the dorsal surface of the dorsal ossification of the braincase (end) can be seen in NMV P179598 (Figs 3, 4). It has a relatively small otic condyle (con) and large auxiliary otic condyle (a.con) on the ascending process. A depression on the dorsal surface, just anterior to the ascending process may be an anterior fontanelle (?fon) as occurs in *Acanthodes* (Miles 1973b).

The palatoquadrate has three separate ossifications, quadrate (Qd), metapterygoid (Mpt) and autopalatine (Aut), as in *Acanthodes* (Miles 1973b, Zidek 1980). Although the jaws of *Howittacanthus* are similar to those of *Acanthodes*, a comparison between the two (Fig. 7) shows that *Howittacanthus* differs in the relative

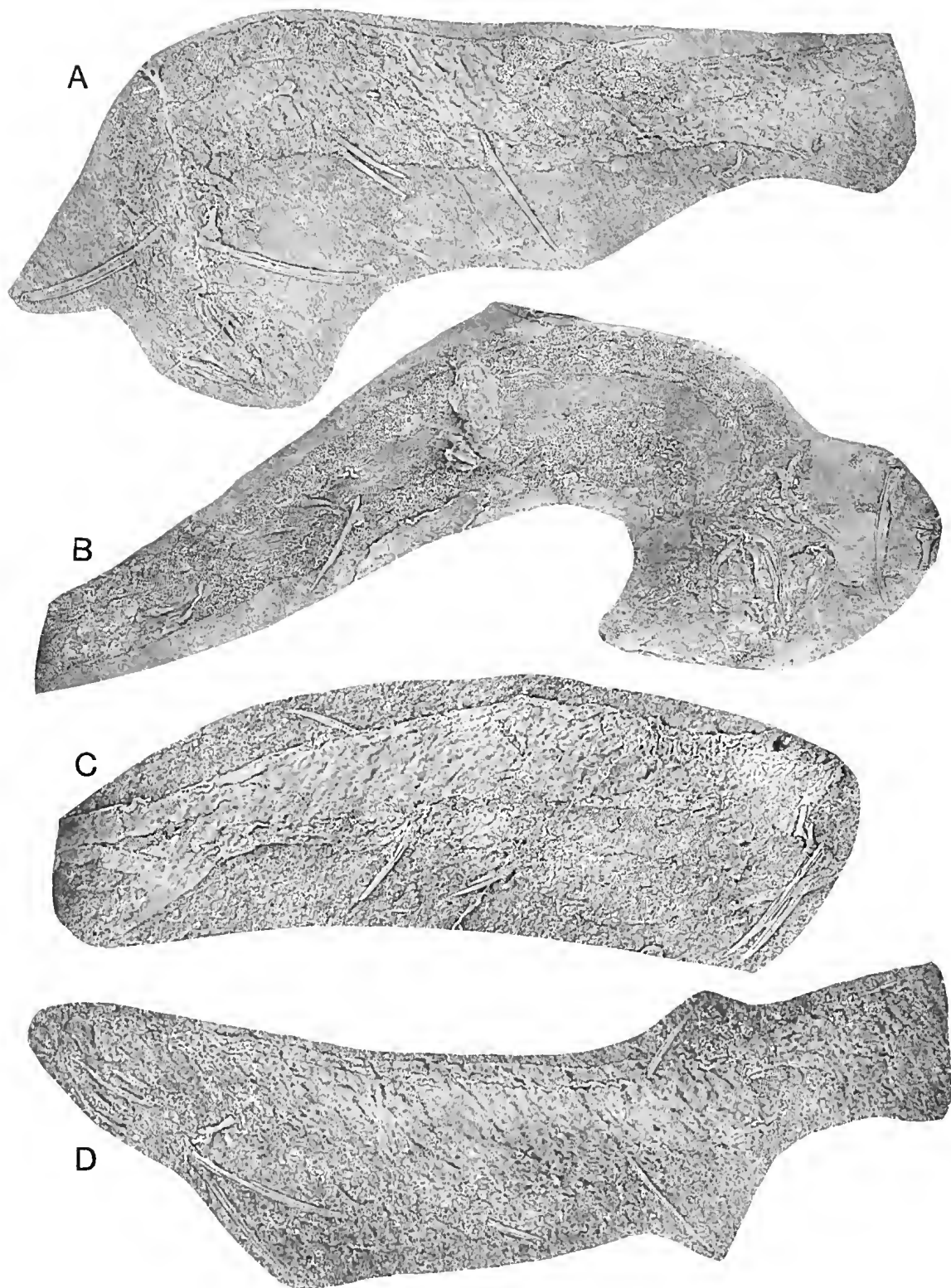


Fig. 1—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. A, holotype, NMV P179580 (X1). B, Paratype, NMV P179582 (X1). C, NMV P179572 (X1.8). D, NMV P179571 (X1.5). Latex casts whitened with ammonium chloride.

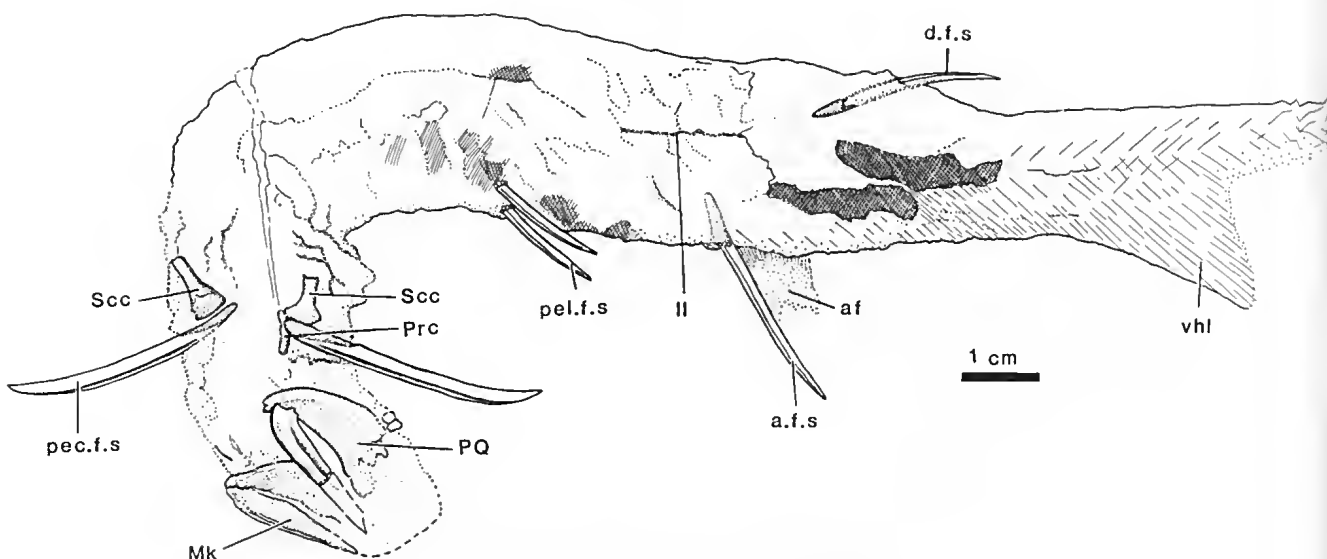


Fig. 2—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. Sketch of holotype, NMV P179580, showing main features. a.con—auxiliary articular condyle; af—anal fin; afs—anal fin spine; a.ot.c—auxiliary otic cotylus; Aut—Autopalatine; ax.l—axial lobe of tail; bas—basal process of autopalatine; BR—branchiostegal rays; con—articular condyle; der—dermal fin ray supports; df—dorsal fin; d.f.s—dorsal fin-spine; dhl—dorsal hypochochordal lobe of tail; dl—dorsal lateral line; end—endocranium (dorsal ossification); epr—exopalatoquadrate ridge; fon—dorsal endocranial fontanelle?; ge—gill chamber; hy—foramen for hyoideus trigeminus nerve; hym—hyomandibular; ll—lateral line; man.b—mandibular bone or splint; mes.l—mesial lamina of scapulocoracoid; Mk—meckelian cartilage; Mpt—Metapterygoid; na—circum nasal bone?; ot.c—otic cotylus; pec.f.s—pectoral fin-spine; pel.f—pelvic fin; pel.f.s—pelvic fin-spine; PQ—Palatoquadrate; Pre—Procoracoid; Qd—Quadrate; See—Scapulocoracoid; sel—sclerotic bones; tess—cranial tesserae; vhl—ventral hypochochordal lobe of tail; vl—ventral sensory line; z1-z4—zones of caudal squamation (after Heyler, 1969).

sizes of metapterygoid to autopalatine bones, the stronger development of a ridge behind the cotyli on the metapterygoid, in the position of the basal process (bas) on the dorsal margin of the autopalatine, and in the shape of the anterior end of the meckelian cartilage (Mk). The quadrate and metapterygoid are closely associated with only a small cartilaginous gap between them which closes up in large individuals (e.g. NMV P179598). The quadrate, the largest of the three upper jaw ossifications, is rather featureless apart from the well-developed extrapalatoquadrate ridge (epr). This continues onto the metapterygoid to terminate as a thickening behind the otic and auxiliary otic cotyli which encloses a foramen, presumably for the ramus hyomandibularis trigemini nerve. The autopalatine is elongated with a strongly-developed basal process situated closer to the posterior end of the bone as opposed to that of *Acanthodes* which forms the anterodorsal corner of the bone (Fig. 7). The metapterygoid and autopalatine ossifications are approximately the same size. The mandibular joint can only be seen in lateral view but appears to be of the normal *Acanthodes*-type with strongly-developed prearticular and articular processes on the quadrate (Miles 1973b, Long in press). The meckelian cartilage was perichondrally ossified as a single unit (NMV P179600, Fig. 5B) and was strengthened by a dermal mandibular splint (man.b) which lies on the ven-

trolateral edge of each jaw ramus. The mandibular splint bears ornamentation of short ridges and grooves oriented posteroventrally to near horizontal in its central section. The anterior end of the meckelian bone is broad with a short straight anterior margin which has a circular symphyseal facet for ligamentous attachment of the opposing jaw (NMV P179598, NMV P179600; Fig. 5B) similar to that in *Acanthodes lundii* (Zidek 1980).

The gill arch rakers (gr) are small conical bones which are found in linear array behind the jaw ossifications (Fig. 4A). They are proportionally smaller than for *Acanthodes* (Zidek 1976, 1980). The branchiostegal rays (BR) are very slender bones which can be seen in several specimens coming from behind the jaw cartilages. The number of rays is hard to estimate as most specimens have the head slightly disrupted with branchiostegals scattered. The number is relatively low compared to *Acanthodes*, and probably similar to *Homalacanthus* (Miles 1966).

The sclerotic ring (sel) is composed of five dermal bones each bearing a very fine ornament of minute tubercles. The anterodorsal and posterodorsal sclerotic bones are the largest elements and these are broader at their contact margin with each other, at the top centre of the ring, than at their ventral borders. The diameter of the whole sclerotic ring when restored is just under half the length of the palatoquadrate.

The endoskeletal shoulder girdle has two ossifications, a short scapulocoracoid (Sec) and a small procoracoid (Prc). There is no evidence in any of the specimens for a dorsal suprascapular ossification as found in *Acanthodes*. The scapulocoracoid (Figs 2, 3A, C, D, E, 4A, 6A, B, D, E) has a slender dorsal division and an expanded ventral mesial lamina (mes. 1) which has a ventral groove for the pectoral fin-spine. The procoracoid (Figs 2, 3C, E, 4A) is a slender curved bone which sits underneath the fin-spine in anterior contact with the scapulocoracoid. The scapulocoracoid is about twice as high as the breadth of the ventral division, with the procoracoid being about two-thirds as long as the long axis of the scapulocoracoid. The fin-spine sat within the ventral groove of the scapulocoracoid which has a well-developed descending mesial lamina that flanks the fin-spine. No foramina are visible on the scapulocoracoid. Overall the pectoral girdle is at a similar level of organization to that of *Cheiracanthus* (Miles 1973a).

All the fin-spines have a single, thick, longitudinal rib along their leading edge, separated from the sides of the spine by well-defined lateral grooves. The fin-spines are quite flat with short, concave posterior faces and

finely-striated insertion areas. The pectoral fin-spine (pec.f.s) is approximately the same size as the anal spine (a.f.s) but considerably broader. The pelvic spines (pel.f.s) are about half as long as the anal spine; the dorsal spine (d.f.s) being only marginally shorter than the anal spine.

The fin webs are partially preserved on some specimens (Figs 1, 2, 5D) permitting estimation of the complete fin shape (Fig. 9B). The pectoral fin (pec.f) is narrow-based with strong radial lineation of the scale rows close to the body. The pelvic fin (pel.f) is long-based, extending back almost to the start of the anal fin, a condition usually found in higher acanthodids such as *Acanthodes* (Zidek 1976) and *Pseudacanthodes* (Denison 1979). Both the dorsal (df) and anal fins (af) are poorly preserved, but appear to run in a straight line back from the tip of the fin-spine to the body to give a broad-based triangular outline.

The caudal fin is well preserved on a few specimens (NMV P179581, P179618; Figs 5A, D, 8). The main axis of the body continues in a straight line to form the axial lobe of the tail, without the tail being angled away from the fusiform body. The axial lobe is very long as it takes

TABLE 1
PROPORTIONS OF *Howittacanthus kentoni* GEN. ET SP. NOV., COMPARED WITH THOSE OF *Acanthodes bridgei* AND *A. lundi* (DATA AND MEASURING POINTS FROM ZIDEK, 1985). n, number of specimens measured.

	n	average	range	<i>A. bridgei</i>	<i>A. lundi</i>
(a) $\frac{\text{Pectoral-anal distance}}{\text{Total specimen length}}$	8	0.43	0.38-0.47	0.42-0.51	0.46-0.52
(b) $\frac{\text{Pelvic-anal distance}}{\text{Total specimen length}}$	8	0.16	0.13-0.21	0.28-0.37	0.38-0.47
(c) $\frac{\text{Prepectoral length}}{\text{Total specimen length}}$	3	0.17	0.13-0.19	0.18-0.24	0.21-0.29
(d) $\frac{\text{Pectoral spine length}}{\text{Total specimen length}}$	7	0.15	0.14-0.17	0.17-0.20	0.15-0.20
(e) $\frac{\text{Pelvic spine length}}{\text{Total specimen length}}$	7	0.065	0.06-0.07	0.07-0.08	0.05-0.06
(f) $\frac{\text{Dorsal spine length}}{\text{Total specimen length}}$	6	0.11	0.10-0.12	0.12-0.14	0.12-0.13
(g) $\frac{\text{Anal spine length}}{\text{Total specimen length}}$	6	0.13	0.12-0.14	0.12-0.14	0.11-0.16
(h) $\frac{\text{Pelvic spine length}}{\text{Pectoral spine length}}$	7	0.44	0.41-0.46	0.17-0.20	0.27-0.35
(i) $\frac{\text{Dorsal spine length}}{\text{Pectoral spine length}}$	5	0.67	0.57-0.75	0.64-0.74	0.62-0.63
(j) $\frac{\text{Anal spine length}}{\text{Pectoral spine length}}$	5	0.80	0.71-0.88	0.64-0.74	0.72-0.77

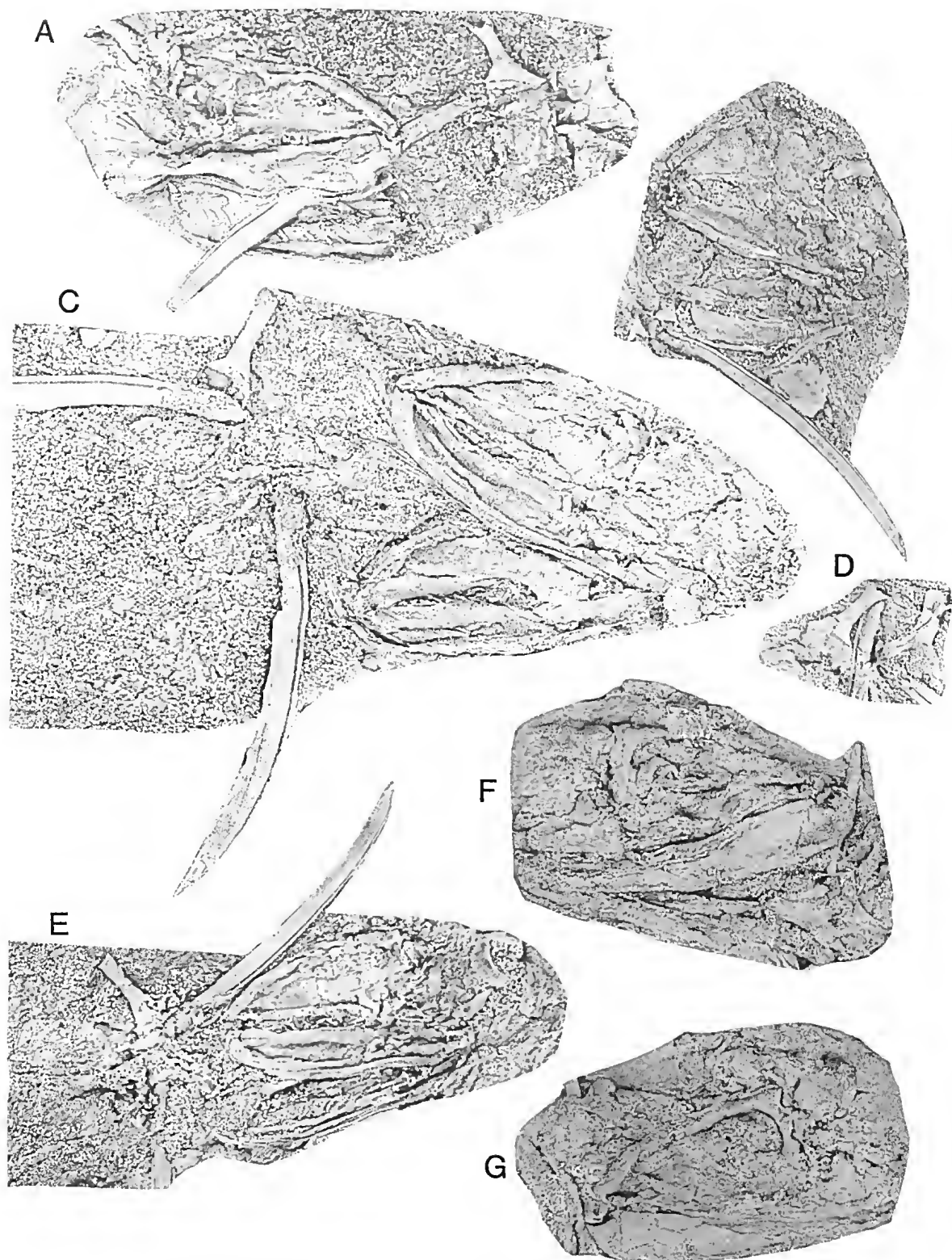


Fig. 3—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. A, NMV P179593 (X2.3). B, NMV P179590 (X2). C, NMV P179586 (X2.5). D, NMV P179603 (X2). E, paratype, NMV P179591 (X2). F, G, lateral views of each side of NMV P179598 (X1.9). Latex casts whitened with ammonium chloride.

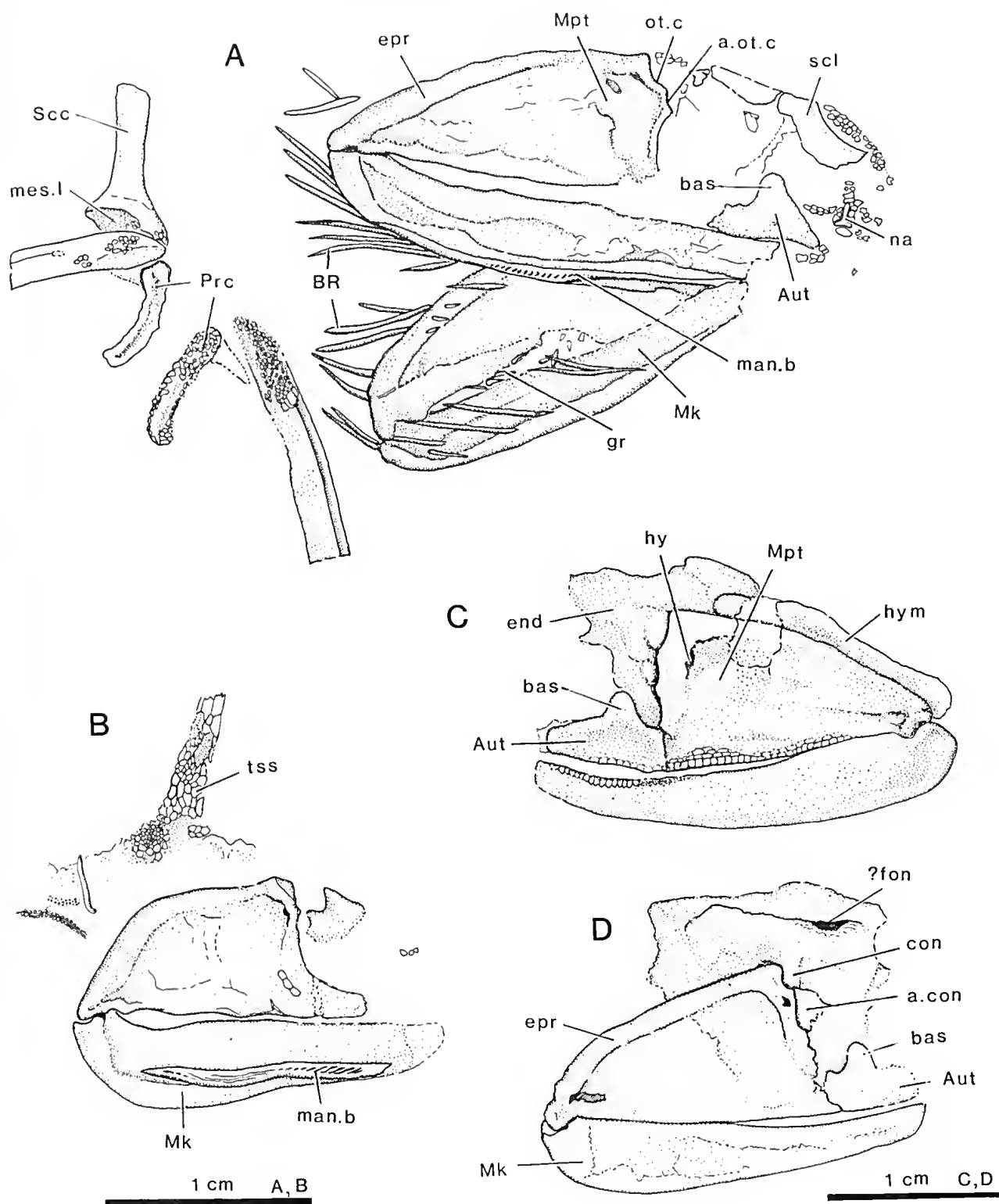


Fig. 4—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. Details of the head and shoulder girdle. A, NMV P179586. B, paratype, NMV P179582. C, D, both sides of NMV P179598. See legend to Fig. 2 for abbreviations.

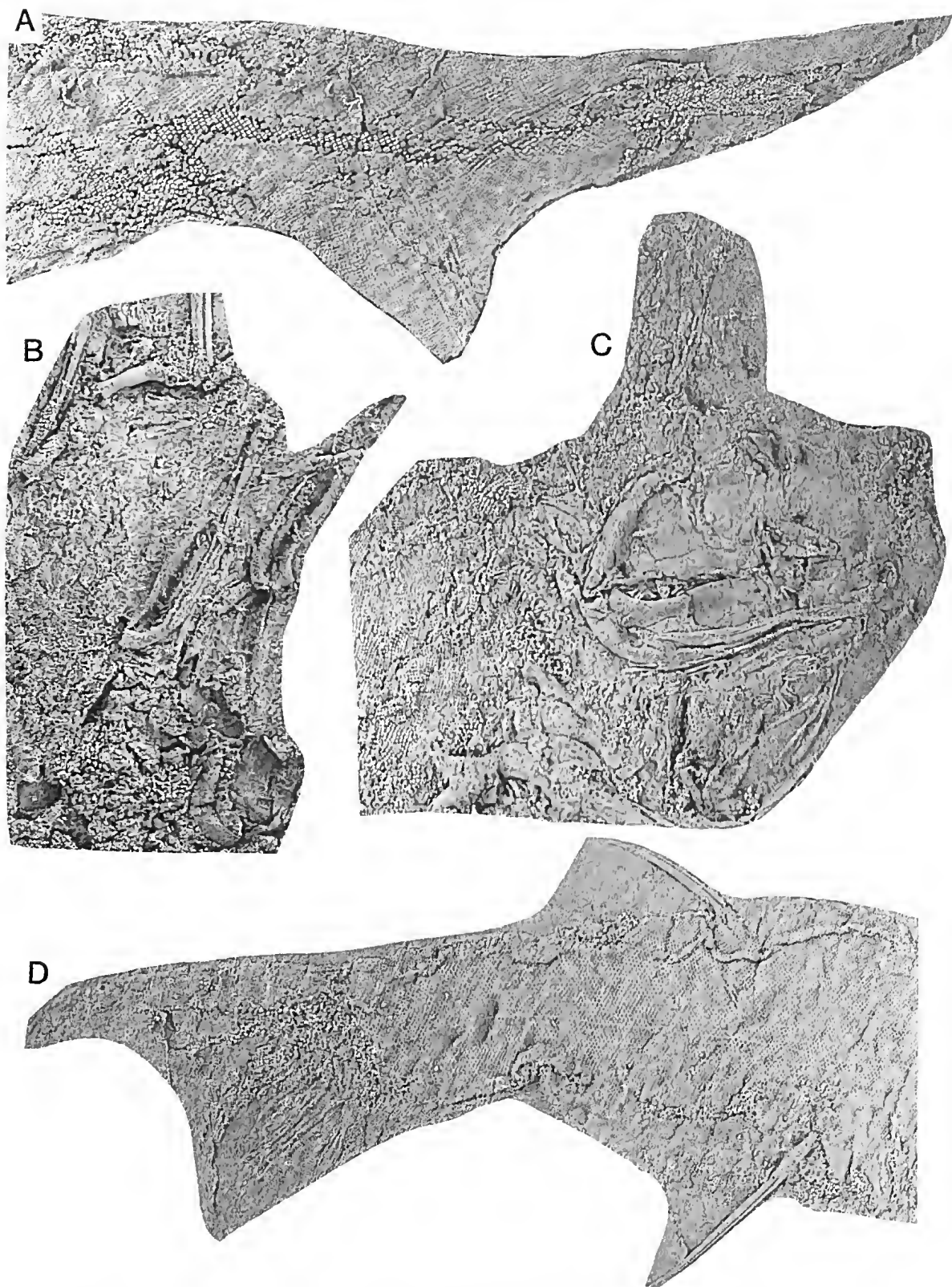


Fig. 5—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. A, tail of NMV P179581 (X2.6). B, NMV P179600 (X2.4). C, paratype, NMV P179582 (X3). D, tail of NMV P179618 (X2.4). Latex casts whitened with ammonium chloride.

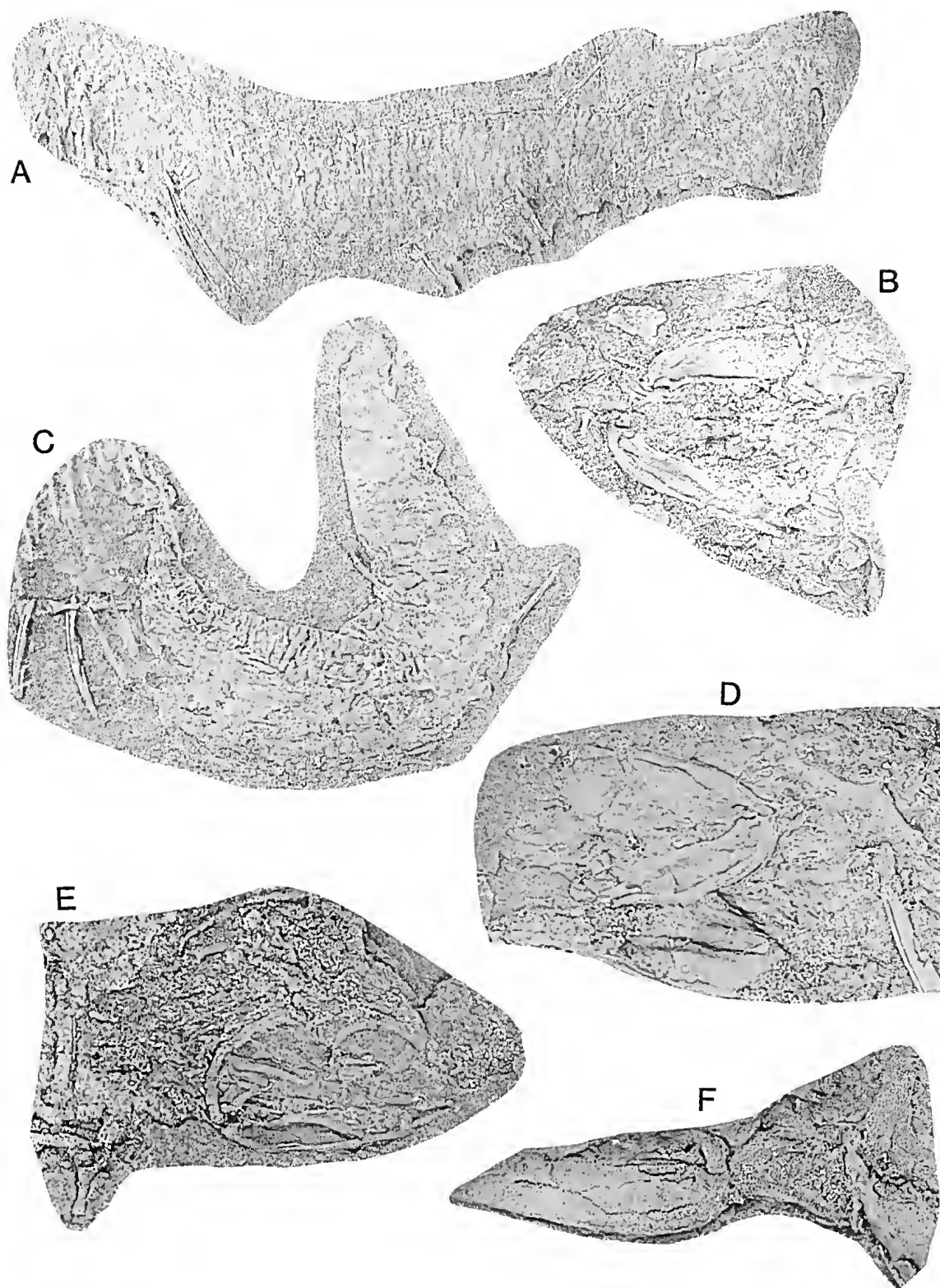


Fig. 6—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria, A, NMV P179576 (X2). B, NMV P179579 (X2.6). C, NMV P179585 (X1.5). D, NMV P179616 (X2). E, NMV P179589 (X1.9). F, NMV P179599 (X2). Latex casts whitened with ammonium chloride.

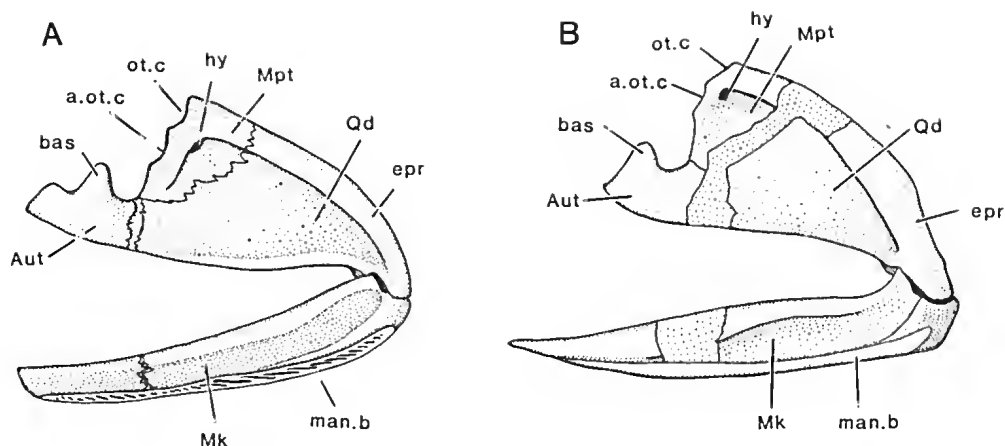


Fig. 7—Comparison between the reconstructed jaws of A, *Howittacanthus kentoni* gen. et sp. nov., and B, *Acanthodes bronni* (after Miles, 1973a). Note particularly the shape of the autopalate and anterior end of the meckelian cartilage. See legend to Fig. 2 for abbreviations.

up approximately one quarter of the total length of the fish. The ventral hypochordal lobe of the tail is relatively short, extending outwards from the main axis of the body for only a third of the length of the axial lobe of the tail. In NMV P179581 (Figs 5A, 8) the squamation of the tail is very well preserved, and shows some Z2 scales present near the base of the main lobe, and development of an additional Z2' zone (as defined by Heyler 1969, also Zidek 1976). Development of Z1, Z3 and Z4 scales are as in *Acanthodes*. Z2' scales are only found on mature specimens (in *Acanthodes*, Zidek 1976) and thus indicate that NMV P179581 represents the mature condition of *Howittacanthus*. At least two specimens (NMV P179581, P179618) show linear ridges (der) radiating out from the main axis of the body to strengthen the ventral hypochordal lobe. These are undoubtedly fin-ray supports or caudal hypurals as described in *Acanthodes* by Miles (1970), although the exact number (at least 9 in NMV P179618) cannot be determined in *Howittacanthus*. The scales of *Howittacanthus* are typically acanthodid and are very small, with a flat, unornamented, rhombic crown, and relatively shallow base, but are indistinguishable from those of *Acanthodes* since the histology of the *Howittacanthus* scales remains unknown.

The laterosensory system is well developed in *Howittacanthus*. The main lateral-line (ll) can be seen running midway along the body depth in many specimens (e.g. Fig. 5D), represented by slight displacement of the scales which forms a ridge along the body surface. A dorsal sensory-line (dl) can be seen as a thick ridge of displaced scales running in irregular fashion close to the anterior margin of the body from the head to just behind the dorsal fin. This feature is most pronounced in juveniles (e.g. NMV P179576, 179572, 179571, 179618; Figs 1C, D, 5D, 6A, B). Little of the sensory-line system can be made out on the head

although some specimens show segments of the preopercular and mandibular lines (e.g. NMV P179598, 179599, Fig. 6F; 179582, Fig. 5C). A ventral sensory line (vl) is also present, seen on NMV P179603 and 179570.

ONTOGENETIC DEVELOPMENT OF *HOWITTACANTHUS*

Measurements were taken only on specimens that clearly showed the particular parameter to be measured, so, although the sample size is small for stated proportions, they are an accurate summary of the range of variation shown by the material. Points used for measurements followed Zidek (1976). Zidek's (1985) recently-published account of the ontogenetic variation exhibited in two species of *Acanthodes* formed the basis for a similar investigation of these ratios in *Howittacanthus*.

The morphology of juveniles does not differ from mature individuals but certain proportional changes occur during ontogeny. Table 1 summarizes proportions for the growth of body sections and fin-spines relative to total length. These findings agree with Zidek's results for *Acanthodes* that the ratios are constant throughout growth, and hence are reliable for use in species diagnosis. Similarly, the ratios of the length of the mandible (meckelian cartilage plus mandibular splint) remains constant at 9-11% total body length, or 18-22% of the pectoral-anal distance. The scapulocoracoid/pectoral fin-spine ratio was also constant through growth, ranging from 22-29% (av: 26%). In the few specimens which permit accurate estimation of the sclerotic ring diameter this was found to be approximately 10% of the pectoral-anal distance, also being constant throughout growth.

Preservation of very small individuals shows that the scale cover was complete over the body on juveniles, rather than absent from the anterior trunk region (Zidek

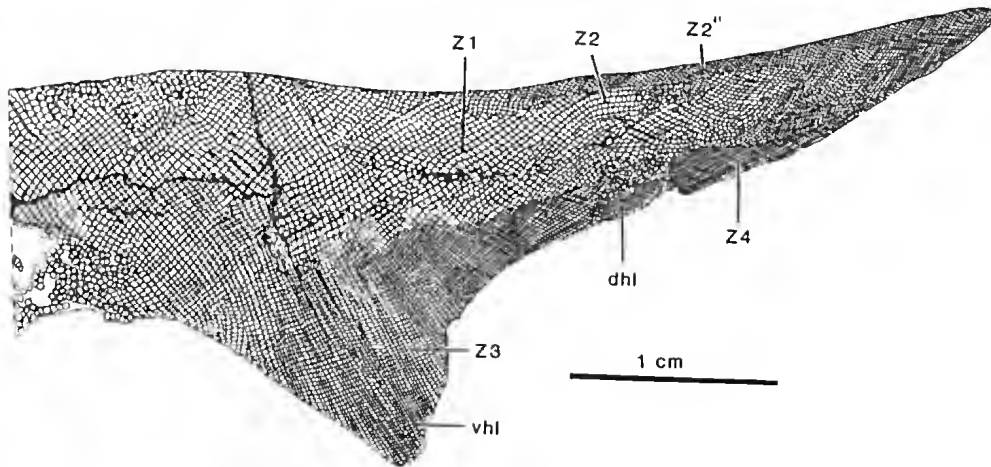


Fig. 8—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. Tail squamation of NMV P179581 (also in Fig. 5A). See legend to Fig. 2 for abbreviations.

1976). The head may have lacked scale cover as it is rarely preserved on the smallest individuals.

RELATIONSHIPS OF *HOWITTACANTHUS*

Long (in press) has discussed the interrelationships of acanthodians, which includes some of the better known acanthodiform genera. Fig. 11A presents a new cladogram of acanthodiforms that includes *Howittacanthus*. Interrelationships of acanthodiforms are difficult to assess because of the high degree of homogeneity in the group. Some of the characters which define the more advanced acanthodiform genera must be regarded as parallelisms which have developed independently in other acanthodian groups (e.g. presence of a procoracoid or loss of one, degree of ossification of the palatoquadrate, reduction of branchiostegal rays).

Howittacanthus is regarded as being more specialized than mesacanthids in having lost the intermediate fin-spines and more specialized than *Cheiracanthus* in having reduced branchiostegal rays. As discussed above, the mesacanthids are here regarded as a plesiomorphic group which is not characterized by any recognizable synapomorphy. Amongst the Cheiracanthidae (Miles 1966), only two genera, *Cheiracanthus* and *Homalacanthus* (Fig. 10G), appear to share synapomorphies. Within the Acanthodida, only these two genera possess scales with several ornamental ribs on the crown, and have lost the dermal mandibular splint. The recognition of these features as synapomorphies assumes that primitively, acanthodiforms possessed scales with flat unornamented crowns (as in mesacanthids and all Acanthodidae), and that the mandibular splint was primitively present in acanthodians (as it is in most elmatiforms, ischnacanthids and acanthodiforms). Primitive characters of cheiracanthids (here including only the two genera under discussion) which are retained are the

presence of a procoracoid in *Cheiracanthus* (or alternatively the loss of one in *Homalacanthus*), and a singular ossification of the meekelian cartilage. Autapomorphic features are the preopercular bone in *Homalacanthus* and the anterior position of the dorsal fin in *Cheiracanthus*.

Within the Cheiracanthidae, as defined by Miles (1966), there are two or three genera which do not show derived characters in common with the two genera discussed above, nor any acanthodid synapomorphies as outlined in the amended familial diagnosis above. These taxa (*Carycinacanthus*, *Protogonacanthus*, and perhaps *Acanthodes ovensi*; Fig. 10C, D, F) should be placed as *incertae sedis* until more knowledge of their anatomy comes to hand. They are clearly more specialized than mesacanthids in lacking intermediate fin-spines, and more so than *Cheiracanthus* in the reduction of their branchiostegal rays, and on these characters I have placed them on the cladogram as the sister group of *Howittacanthus*, *Acanthodes*, and *Acanthodopsis* (with *Pseudacanthodes* and *Traquairichthys* tentatively included).

Acanthodes and *Howittacanthus* are the best known taxa within the Acanthodidae, with *Pseudacanthodes* and *Traquairichthys* undoubtedly belonging to the family but relatively poorly known (Denison 1979, Jensen 1975). *Acanthodopsis* is referred to the Acanthodidae by Long (in press) on shared characters of the metapterygoid and mandibular joint. *Howittacanthus* uniquely shares with *Acanthodes* and *Acanthodopsis* a metapterygoid with both otic and auxiliary otic cotyli, and a palatoquadrate ossified in maturity as three separate parts. Other typical acanthodid features of *Howittacanthus* are the singularly-ribbed fin-spines and partial ossification of the braincase (otherwise seen only in *Acanthodes* and here regarded as a possibly derived condition). I conclude that *Howittacanthus* is the sister group to *Acanthodes* plus *Acanthodopsis* (and tentatively *Traquairichthys* and

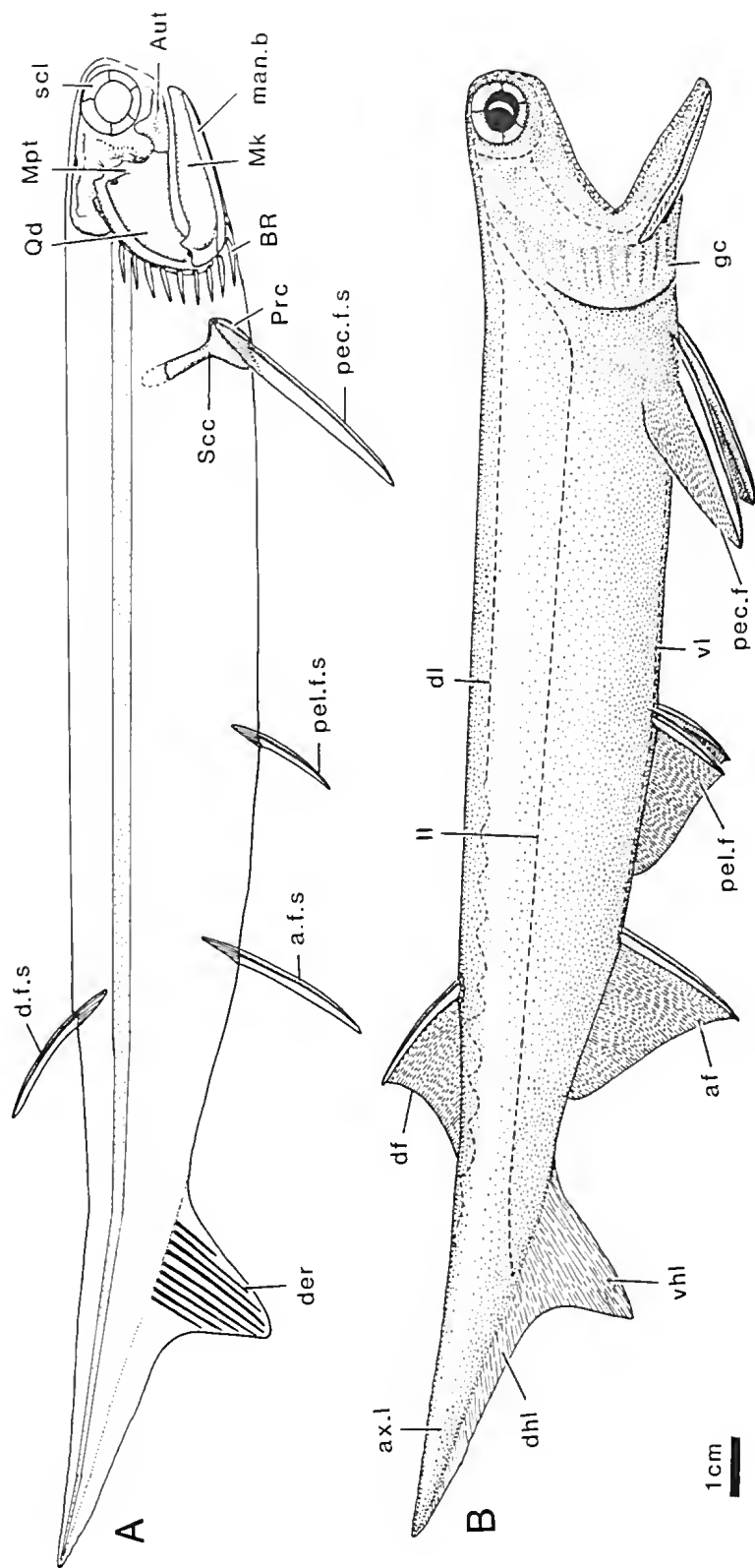


Fig. 9—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. A, attempted reconstruction of the fish showing known ossifications of the body (fin ray supports not actually seen). B, attempted life restoration of the fish in feeding position with mouth open. See legend to Fig. 2 for abbreviations.

Pseudacanthodes). *Traquairichthys* and *Pseudacanthodes* are derived acanthodids which share with *Acanthodes* specialization of the pelvic fin: anterior position of the pelvic fin (*Pseudacanthodes*) or loss of the pelvic fin entirely (*Traquairichthys*). Until more is known of the jaw structures in these genera I suggest that they be placed tentatively as the sister group to *Acanthodes*, *Howittacanthus* and possibly *Acanthodopsis* as they show reduction of the brachioistegal rays and elongated gill chambers. *Acanthodes ovensi*, recently redescribed by Forey and Young (1985), does not show the characteristic placement of the pelvic fin closer to the pectoral as in other species of that genus (*A. bridgei*, Zidek 1976; *A. sulcatus*, Miles 1971; *A. hndi*, Zidek 1980). *Acanthodes ovensi* differs from all other acanthodids except *Acanthodes* and *Pseudacanthodes* by its relatively long pelvic fin web, and from these genera by the position of the pelvic fin-spine, and should probably be referred to a new genus.

SOME COMMENTS ON ACANTHODIAN BIOGEOGRAPHY

Until recently our knowledge of Gondwana acanthodians was poor, and little could be said of their zoogeographic significance. Young (1984) discussed the underlying assumptions and criticisms of Palaeozoic vertebrate zoogeography. The aim of this discussion is to utilize available palaeogeographic data (continental reconstructions based on empirical geological data) in an hypothesis to explain the known distribution of certain acanthodians. Any inferences to area connections can only be tentative in the light of changing and dissimilar views of Palaeozoic continental reconstructions (e.g. Scotese *et al.* 1979, Heckel & Witzke 1979, Riekard & Belbin 1980). Phylogenetic analysis of the Acanthodii, considered in relation to area cladograms, should then suggest where paraphyletic "stem groups" may have originated. The evidence for such an analysis is based on the known occurrence of species in time and space, and recognizable absences of taxa from sites which contain diverse and well-preserved faunas. Biogeographic provinces proposed by Young (1981) are referred to in this discussion.

The oldest reliable report of acanthodians comes from the Early-Middle Silurian of China (Pan Jiang 1983). The Ordovician acanthodian spine from Girvan, Scotland (Harper 1979) has been queried by Dr. Alex Ritchie and may be arthropodan (Blicek *et al.* 1984, p. 854). The Silurian distribution of acanthodians indicates that the group was then widespread, occurring in the Euramerican Province (Gross 1947), South China Province, East Gondwana (south-eastern Australia, Turner & Pickett 1982) and possibly from central Gondwana and the Birman Block (age not certain; Blicek *et al.* 1984, Gupta & Turner 1973). All of these occurrences include "*Nostolepis*"-type scales. Only ischnacanthid and elmatiform acanthodians have been recorded from the Silurian.

The acanthodiforms first appear in the Lower Devonian of Britain and Scotland (Watson 1937, Miles 1973a), represented by one genus, *Mesacanthus*, from facies indicative of fresh water habitats (Allen & Tarlo 1963). Diverse, well-preserved faunas of Lower Devonian age from China suggest the group was absent from this region (e.g. Wang Nicnzhong 1984), although few faunas of this age (and facies) are known from Australia. In this case, the absence of acanthodiforms from the East Gondwana Province during the Lower Devonian cannot be confirmed, although they appear to be absent from the *Wuttageoonaspis*-fauna reported by Ritchie (1973) and Turner *et al.* (1981). *Mesacanthus* has been shown above to be one of the plesiomorphic "stem group" acanthodiforms. Middle Devonian acanthodiforms are also restricted to the same biogeographic province, Euramerica, but are more diverse (*Cheiracanthus* spp., *Mesacanthus* spp., plus indet. scales such as *Acanthodes? dublinensis*; Gross 1973, Denison 1979). Thus the earliest and most plesiomorphic acanthodiforms as currently known appear to be endemic to the Euramerican Province, and a centre of origin for the group would be expected here. In the early Late Devonian the group is recorded for the first time from a definite marine habitat (*Protogonacanthus*, Bergisch-Gladbach limestones, Germany, Miles 1966), and from an area geographically widely separated from the earlier Euramerican occurrences (East Gondwana Province, *Howittacanthus*). These two events may be causally related: invasion of marine habitats followed by dispersal and then re-entry into new freshwater habitats. Acanthodid distribution during the Late Devonian-Permian appears to represent a simple progression-rule type of dispersal following a long period of endemism in Euramerica. *Acanthodes* (Carbo-Permian) is the first widespread genus known to occur in both marine and continental facies (Zidek 1976, Denison 1979). Apart from Euramerica, this genus is known to occur from Gondwana (South Africa, Gardiner 1973; Australia, Woodward 1906) and South China (Wang & Turner 1985), although doubt must be cast on the last of these reports as it is based on scales alone. Fig. 11B shows a schematic biogeographic history of the acanthodiforms, which clearly illustrates the widespread dispersal of the higher acanthodids during the Late Devonian and Carboniferous.

Climatiforms and ischnacanthids are widespread at their earliest appearance and flourished during the Lower Devonian particularly in Euramerica and Baltica (Miles 1973a, Bernacsek & Dineley 1977, Schultz & Zidek 1982). The diplacanthoid climatiforms are common in the Middle Devonian in Euramerica (*Diplacanthus* spp.) where they survived on to the Late Devonian (*D. horridus*, Frasnian). By the start of the Late Devonian they were also in East Gondwana, represented by a highly specialized genus, *Culmacanthus* (Long 1983). Culmacanthid cheek plates belonging to other species are now known also from the Pambula River fauna (south coast N.S.W.) and from the Devonian of Antarctica (Dr. G. Young, pers. comm.) indicating that they are probably an endemic East Gondwana group.

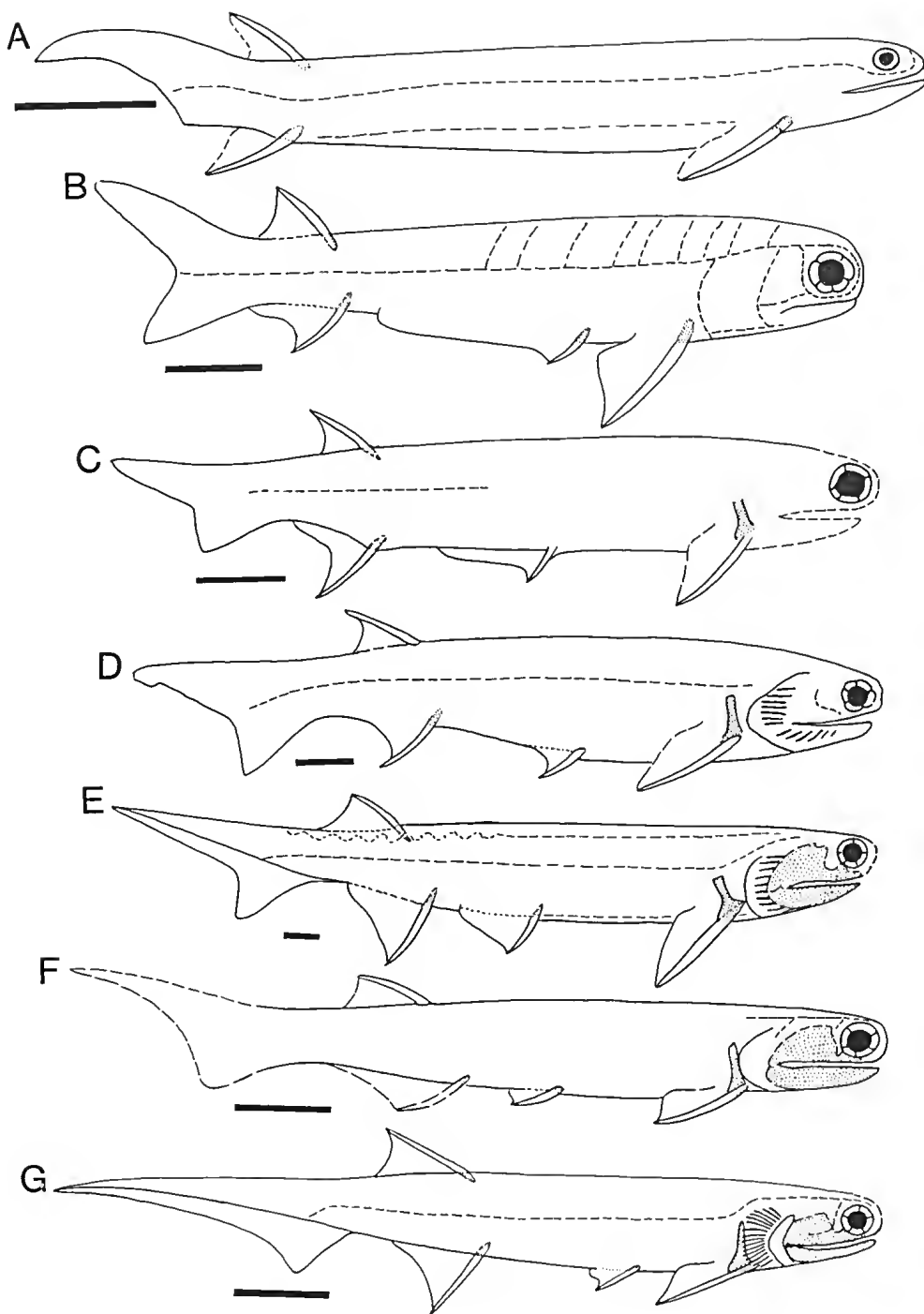


Fig. 10—Comparison of body morphology of certain higher acanthodiforms. A, *Pseudacanthodes* (Late Carb., Europe). B, *Acanthodes bridgei* (Late Carb., U.S.A.). C, *Acanthodes ovensi* (Early Carb., Scotland). D, *Carycinacanthus* (Early Carb., U.S.S.R.). E, *Howittacanthus* (Late Dev., Australia). F, *Protogonacanthus* (Late Dev., Europe). G, *Homalacanthus* (Late Dev., Canada). All except C and E after Denison (1979). C, after Forey & Young (1985). E, original. One centimetre bar scale.

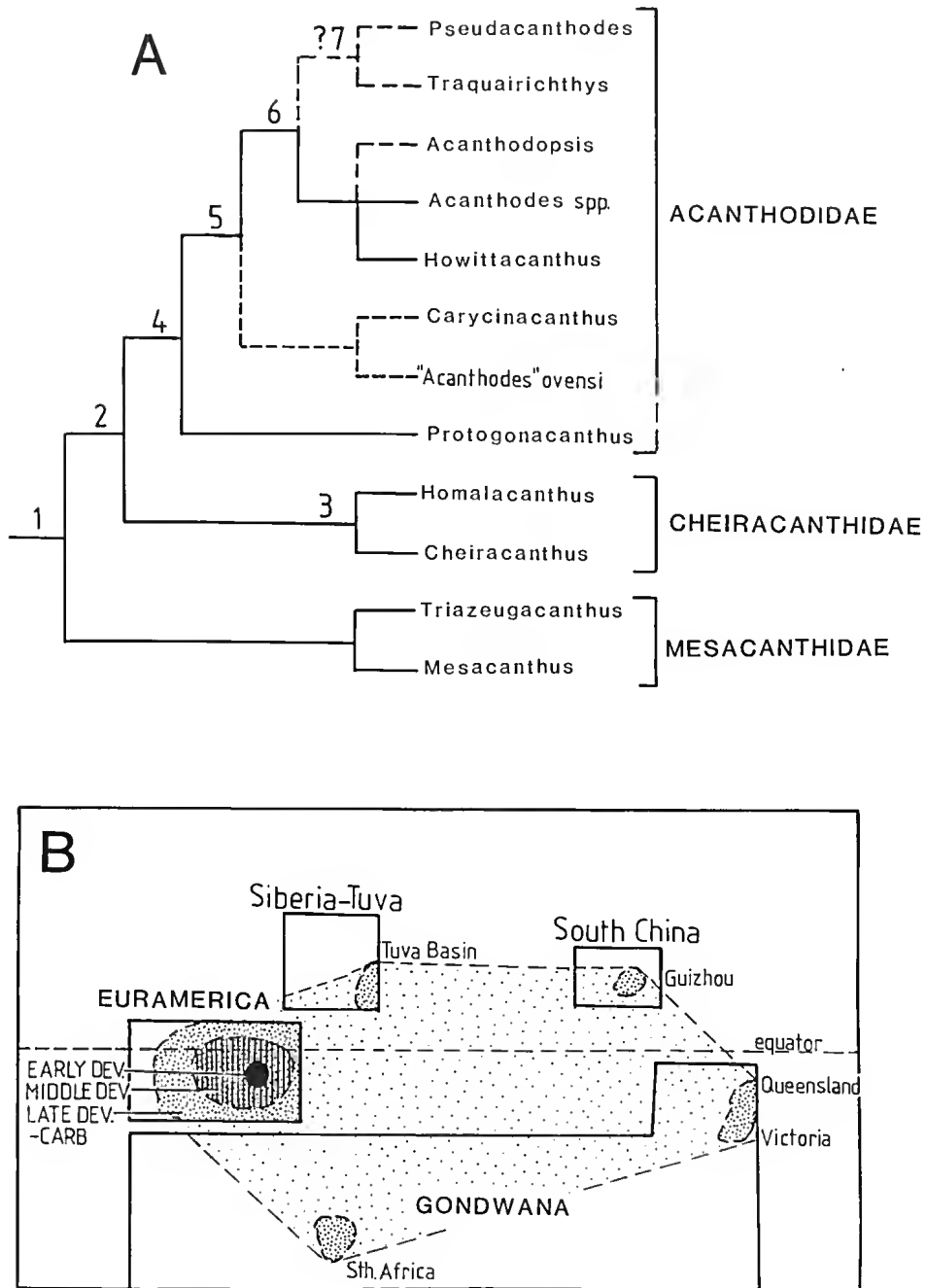


Fig. 11—A, hypothesis of acanthodiform interrelationships. Dashed lines represent tentative phylogenetic position of certain taxa for which complete anatomical data are lacking. Familial groupings according to this paper. Numbered synapomorphies: 1, single dorsal fin; scales with flat-topped unornamented crowns and *Acanthodes*-type histology (assumed for *Howittacanthus*). 2, loss of intermediate fin-spines. 3, scales with ornamented crowns; loss of mandibular splint. 4, branchiostegal rays extending only halfway across length of gill chamber. 5, fin-spines with single rib (assumed convergence with *Homalacanthus*); relatively long based pelvic fin. 6, palatoquadrate ossified in three parts; metapterygoid with both otic and auxiliary otic cotyli. ??, modification or loss of pelvic fin. B, distribution of the Acanthodidae in space and time, showing dispersal area of the higher acanthodids in the Late Devonian and Carboniferous (light stipple). Provinces (after Young 1981) indicated only to show extreme range of acanthodids.

Similarly, gyraacanthid climatiforms are found in the Lower and Middle Devonian of Euramerica (including southern Europe; Denison 1979) but first become widespread in the Late Devonian and Carboniferous, where they have been recorded from South Africa (Chaloner *et al.* 1980), Antarctica (White 1968) and Australia (Woodward 1906) represented by the endemic Gondwana genus *Gyracanthides*. Isehnacanthids show no clear pattern of dispersal, and their interrelationships are poorly known (Long in press). In the Early Devonian they are found in Euramerica (Watson 1937, Miles 1973a, Bernaeseck & Dineley 1977, Ørving 1957), South China (Wang Nienzhong 1984) and East Gondwana (Long in press). From the complexity of the dentition it would appear that the most specialized ischnacanthids could have been those from the Emsian of south-eastern Australia. The stem group ischnacanthids are probably represented by "*Nostolepis*"-type jaws from the Silurian of Oesel because of their simple construction and the primitive nature of associated "*Nostolepis*"-type scales (Ørving 1967, Denison 1976, 1979); and by Early Devonian taxa with simple dentition such as *Uraniacanthus* (Miles 1973a, Long in press). Similarly *Machaeracanthus*, recently discovered from the Devonian of Antarctica (Dr. G. Young, pers. comm.) represents another acanthodian which is widespread by the Middle Devonian and may have come from a group which had its origin elsewhere from Euramerica. This genus may be an ischnacanthid (Zidck 1975) which would be consistent with the occurrence of other "specialized" ischnacanthids from the Emsian of Australia (Long in press). The ischnacanthids which appear to have reached a high level of organization (from dentition alone) by the Emsian, and were known to be in East Gondwana and South China may not have originated in Euramerica as the group is known from Silurian age in Euramerica, China and Australia. Isehnacanthids might be expected to show a completely different distributional pattern from acanthodiforms or the certain climatiforms discussed here.

The distributional patterns of acanthodids, gyraacanthids, and diplacanthoids is consistent with that described by Young (1981) as a generalized model for Devonian vertebrates, incorporating an episode of faunal interchange between East Gondwana and Euramerica sometime between the end of the Early Devonian and the early Late Devonian. The presence of these groups in Euramerica until the Late Devonian would imply that either a biological change occurred independently in each group (such as the invasion of saltwater) or that a geographical change occurred which affected all of these groups. Prediction of a geographical change, like the breakdown of a barrier, could be tested by the distribution of other taxonomic groups (vertebrates, invertebrates, plants). Further study of Devonian biotic distributional patterns is required.

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RAINFALL AND WATER YIELDS OF THREE SMALL, FORESTED CATCHMENTS IN NORTH-EAST VICTORIA, AND RELATION TO FLOW OF LOCAL RIVERS

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ABSTRACT: The rainfall and water yield of three small, contiguous forested catchments (0.46 to 1.13 km²) in north-eastern Victoria were compared. Consistent differences of up to 10% in rain gauge catch over short distances were observed. In wet periods, the catchments may return 60% or more of rainfall as streamflow. When annual rainfall is below about 700 mm, streamflow effectively ceases. Two of the catchments show evidence of water loss relative to the third; this is approximately proportional to the streamflow and varies from about 0.2 mm per day in the driest period to about 2.5 mm per day in the wettest period. The small streams all show similar seasonal variation to the nearby Buffalo, Dandongadale, and Rose Rivers, while the water yields per unit area of the river catchments are quite similar to the two "leaky" catchments. However, inadequacies in the rainfall information in these preclude water balances. It is concluded that the seasonal variation of the small streams can be regarded as broadly representative of the larger rivers in this environment, with deviations likely to be due to unknown meteorological factors.

The rationale behind small catchment research is that other catchments of similar size in the same environment will respond to meteorological inputs similarly, and that the response of the larger catchments in the area is at least not dissimilar to that of the smaller catchments. However, because of the expense and difficulty in obtaining data sets of adequate quality there is relatively little specific information on this matter in Australia. The purpose of this study was to examine the water yield of three small, forested catchments (0.46-1.13 km²) in north-eastern Victoria, and to compare this to that of three larger catchments (176-425 km²) in nearby and somewhat similar environments. The three small catchments (Clem, Ella, and Betsy Creeks) comprise the Cropper Creek Hydrologic Project Area of the Department of Conservation, Forests & Lands; this was established to provide hydrologic information on forest practices. The three larger streams are the Buffalo River (at Abbeyard), and the Rose and Dandongadale Rivers near their confluence ("Matong North"). These rivers were selected because gauging records were available and the flow records were unaffected by the influence of substantial irrigation diversion, river regulation, or agricultural developments. Table 1 gives details and Fig. 1 shows the locations of the catchments. Fig. 2 gives a plan of the Cropper Creek Project Area, a description of which can be found in Bren *et al.* (1979). In 1980, Clem Creek catchment was converted to radiata pine (*Pinus radiata* D. Don) to study the effects on water yield, peak flows, sediment yields, and nutrient budgets. This work is based on the pretreatment data.

SMALL CATCHMENT HYDROLOGY

The small catchments have a dry sclerophyll open forest that generally has little merchantable timber. The bedrock consists of a tightly folded, fractured, and

steeply dipping sequence of Ordovician sediments. The overlying soils have a high permeability and low erodability. They are shallow on the ridges with a high surface cover of fractured rock, while gully soils are deep loams formed from transported slope deposits. A number of studies have examined aspects of the hydrology of the small catchments, with a summary of these reported in Bren and Turner (1985). These studies considered slope hydrology, groundwater movement, stream-channel hydraulics, and runoff generation. The work showed that streamflow mainly resulted from groundwater discharge emanating from porous catchment slopes. This groundwater is recharged by rainfall and is stored in the weathered rock zone. The small streams commence as rather elongated "springs". The rainfall response is complex and varies with distance downstream from the spring. At the springhead the flow varies only slowly during rainfall, reflecting a stabilising effect due to the convergent, semi-circular springhead catchment. Most of the more rapid variation in streamflow results from subsurface flow entering from the catchment flanks. This behaviour is discussed in detail in Bren and Turner (1985).

Hewlett, Fortson and Cunningham (1984) included rainfall and runoff data from Clem Creek in a study of storm flow responses from small forested catchments located in humid environments. The data set also included 14 catchments from North America and two from South Africa. The analysis showed that, on virtually all catchments, the most important predictor of the storm response was the storm rainfall. Knowledge of short-term rainfall intensities (e.g. maximum 1 h rainfall intensity, etc.) gave little improvement in predictions of storm response provided the storm rainfall was known. An inference drawn from this study is that relatively short-term variations in rainfall intensity have little influence on the resultant runoff compared to the total volume of storm

TABLE 1
CHARACTERISTICS OF THE STUDY CATCHMENTS

	Small Catchments	Large Catchments
Gauging Stations	120° V-notch weirs with water level recorder.	Buffalo R. — Natural control Dandongadale R. — Concrete weir Rose R. — Concrete and rock weir
Catchment Area	Clem Ck — 0.46 km ² Ella Ck — 1.13 km ² Betsy Ck — 0.44 km ²	Buffalo R. — 425 km ² Dandongadale R. — 181 km ² Rose R. — 176 km ²
Private property	Nil	Buffalo R. — 24 km ² Dandongadale R. — Nil Rose R. — 56 km ²
Gauging Authority	Dept. Cons., For. & Lands.	Rural Water Commission
Catchment Vegetation	Dry sclerophyll vegetation with mainly peppermint species & well developed gully vegetation	Largely dry sclerophyll with small areas of agricultural land and some alpine areas in catchment headwaters.
Catchment Topography	Moderately steep.	Moderately steep to steep foothills; some mountainous areas at heads of rivers
Land Use	Non-commercial forest.	Mainly non-commercial forest with some agriculture and logging.
Rainfall Stations	5 within Project Area Ella Creek gauge used in study.	No reliable stations in catchments
Precipitation	Rain, occasional light snow.	Rain, winter snow in upland areas.

rainfall. Of particular interest was the statistical similarity of the rainfall response of all catchments.

Bren and Turner (1979) measured overland flow on the catchment slopes during storm rainfall and found that it was small and, at best, could only account for less than 5% of the measured stream flow response during storm rainfalls. More typically it was less than 1%, and most of the overland flow measured appeared to be associated with raindrop splash. The lack of overland flow appeared to reflect the high infiltration capacity of the slopes relative to the rainfall intensities encountered in this environment. Vertessy (1984) carried out a similar study in a burnt eucalypt forest near Warburton (Vic.), and obtained similar results.

Bren and Leitch (1985) examined the water yield ("runoff") from a stretch of forest road near the project area. The flow from a road drainage culvert was passed through a measurement weir, and then discharged

TABLE 2
REGRESSION EQUATION OF CLEM CREEK MEAN DAILY FLOW (C, l/s) AS A FUNCTION OF ELLA CREEK (E) AND BETSY CREEK (B) MEAN DAILY FLOWS (l/s), AND RATIO OF THE CORRESPONDING CATCHMENT AREA

Regression equation	Ratio of catchment areas	Correlation coefficient
$C = 0.473E + 0.714$	0.41	0.985*
$C = 1.06B + 2.041$	1.04	0.952*

* Denotes significance of the correlation coefficient at $P = 0.001$.

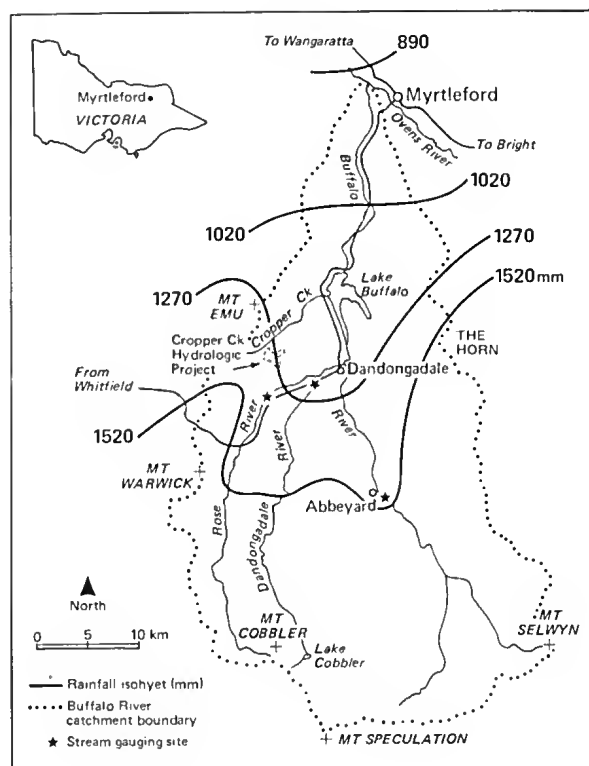


Fig. 1 — Plan showing the location of the Cropper Creek Project area in relation to the Buffalo River catchment, and approximate location of isohyets.

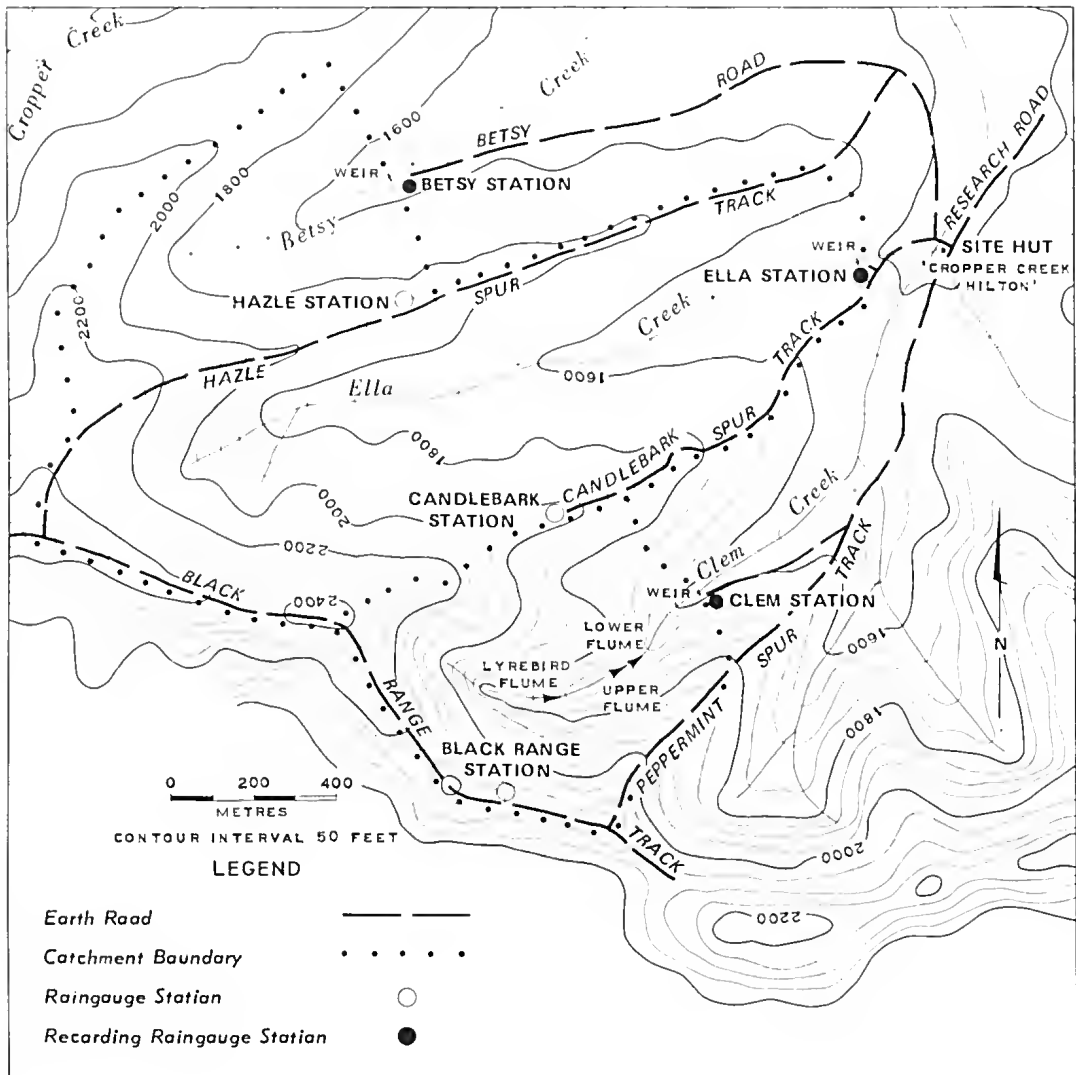


Fig. 2—Plan of the Cropper Creek hydrologic project area.

uniformly over a 5 m width of slope. Some 5 m downslope, a collection gutter collected surface flow and again passed this into a measurement weir. Continuous records of above-road runoff and rainfall intensity were also maintained. The volume of storm runoff attributable to a given storm rainfall ("stormflow") per unit road area was best predicted by the depth of rainfall, while the peak flow per unit road area was best predicted by the maximum 1 h rainfall intensity. The results were compared with the models of stormflow and peak flow generation derived by Hewlett, Fortson and Cunningham (1984) for Clem Creek. It was concluded that the presence of a length of road in this catchment would lead to a small increase in stormflow for small and moderate storms but would make little difference for larger storms. However, the road would possibly make a substantial contribution to the peak flow achieved for all

storm-sizes, although timing differences in reaching peaks could be a complicating factor. A theoretical analysis showed that a road which occupied 2% of Clem Ck catchment area and discharged waste water into the stream would give about 10% more stormflow but would often double the peak flow generated, although the relative effect diminished with storm size. The passage of runoff across a short length of natural forest slope appeared to make little difference to the flow, despite the known high infiltration capacity of undisturbed slopes and the unsaturated state of the soil. Observation suggested that the fine sediment carried by the water quickly blocked infiltration pathways into the soil. It was concluded that if infiltration of the outflow of road culverts is to be obtained then special measures to adequately distribute the water over the slope and to maintain infiltration pathways may be necessary.

THE LARGER CATCHMENTS

The topography and vegetation of substantial tracts of the lower parts of the three larger catchments are similar to those of the smaller catchments. The Land Conservation Council (1974) ascribe the same vegetation types (variants of "open peppermint forest") to virtually all the catchments, with the exception of small areas of montane forests in the vicinity of Mt Cobbler and Mt Selwyn. The upper tracts of the rivers tend to be more mountainous and rocky than the Cropper Creek area. It is concluded that the Cropper Creek catchments are similar to the most common land-type in the larger catchments. Although both the Rose and Buffalo Rivers have blocks of private property (Table 1) much of this is uncleared or semi-cleared only.

The streamflow data were collected by the Rural Water Commission as part of their river gauging projects.

DID UNUSUAL RAINFALL PATTERNS OCCUR DURING THE STUDY?

The rainfall and streamflow data for the small streams were collected as part of the Cropper Creek Hydrologic Project and cover the period from its inception (1975) until the end of the pre-treatment phase (1980). Because of the sparseness of settlement in the larger catchments there is no continuous record of rainfall within or of variation across the catchments, with the nearest elevated stations being at Mt Hotham or Mt Buller. Fig. 1 shows isohyets estimated by the Land Conservation Council (1974), indicating a substantial rainfall gradient across the Buffalo River catchment. It is concluded that the rainfall measured at Cropper Creek is likely to be a good indicator of relative rainfall variation over time, but that it will underestimate precipitation on the larger catchments by an unknown factor.

Fig. 3 shows the historical (1897-1979) distribution of annual rainfall at Myrtleford and the rainfall during the period of measurement. Analysis of these data and the 1975-9 rainfall data collected at Ella Creek Weir shows that:

- i. there is a 2.9% probability of annual rainfall being higher than the highest experienced during the study period and 15.0% probability of lower than the lowest during the study period;

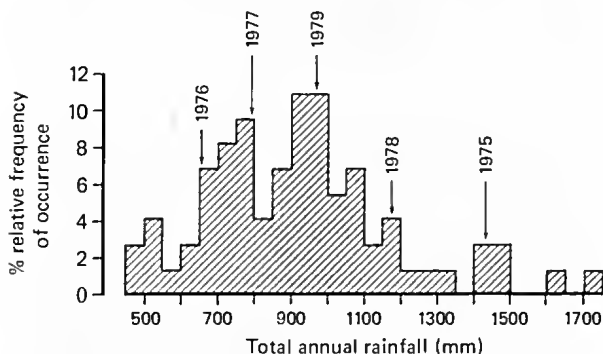


Fig. 3—Historical distribution of rainfall (1897-1977) at Myrtleford, and rainfall during the period covered by this study.

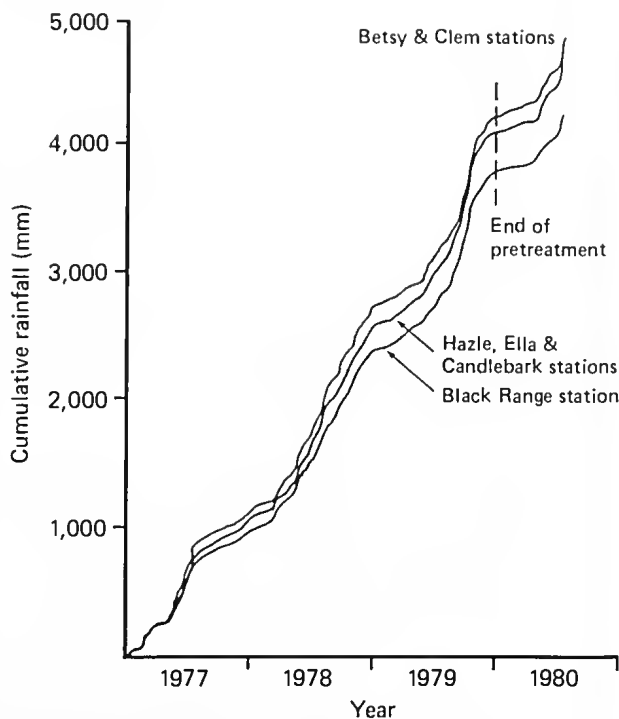


Fig. 4—Cumulative rainfall at measurement stations within the project area from Jan. 1977 to July 1980.

- ii. monthly rainfall at Ella Creek was well correlated ($r^2=0.923$) with rainfall at Myrtleford, and about 38% higher, confirming the rainfall gradient shown on Fig. 1;
- iii. the frequency distribution of one day rainfalls at Myrtleford during the study period was close to that of the historical distribution, but the frequency distribution of substantial two and three day storms showed that these were slightly under represented in the 1975-79 data;
- iv. no absolute extreme one, two, or three day rainfalls occurred during the study period although substantial local flooding occurred on a number of occasions; and,
- v. within the project area consistent differences of up to 10% in gauge catch were recorded. Fig. 4 shows the cumulative rainfall at the various stations for a 30 month period. There is a very constant relativity between gauges, but this cannot be easily related to elevation or topography, although the more elevated gauges do appear to receive less rainfall. It is not known whether such differences were due to gauge exposure or reflected real variations across the catchments. Corbett (1967) showed that such variation can be regarded as "normal". The Ella Weir gauge gave a reading about the mean of all gauges and hence has been used in this study. The implications of this variation are discussed below.

We concluded that the historical rainfall distribution with time was reasonably sampled during the measurement period, and that it was unlikely that any of the

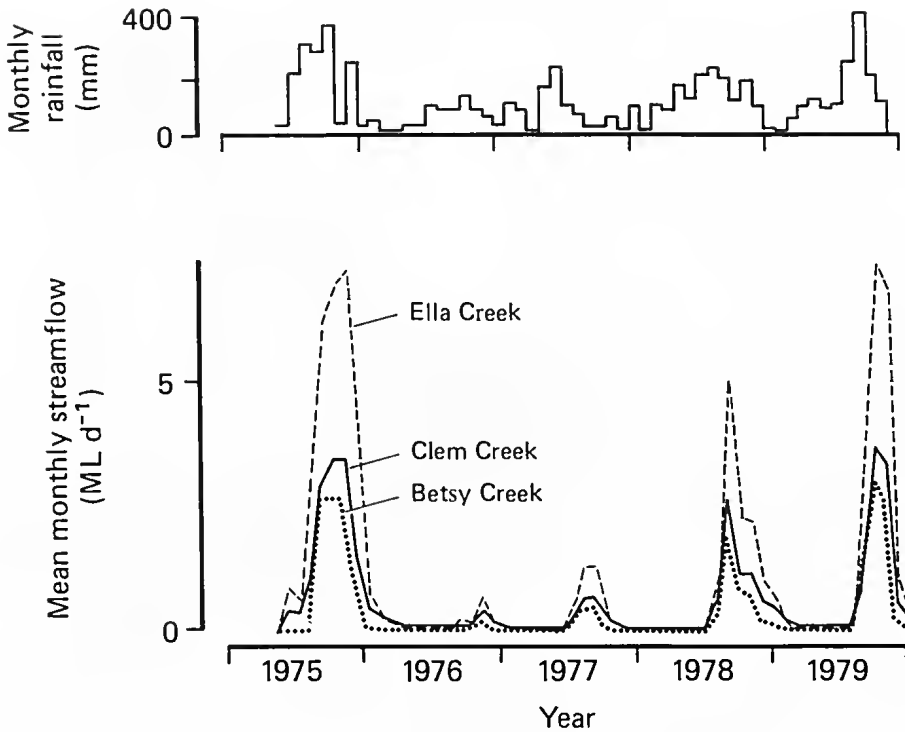


Fig. 5—Rainfall and mean monthly streamflow at Cropper Creek.

findings reported here are attributable to anomalies in the rainfall events.

SEASONAL VARIATION OF STREAMFLOW AT CROPPER CREEK

Fig. 5 shows the rainfall at Ella Ck Gauge and the streamflow (averaged over calendar months) of all streams. The annual pattern is of high winter and spring flows combined with low (or absent)? summer and autumn flows. Only Clem Ck exhibited sustained flow, while the two other streams had a propensity to dry up in summer. Ella Ck would usually cease flowing in early summer and recommence flowing after a substantial storm (c. 100 mm) occurred in autumn, and Betsy Ck would usually only flow in reasonably direct association with sustained substantial rainfall. However, once flowing, their rainfall response was approximately proportional to the catchment size. Table 2 shows regression equations of average daily flow in Clem Ck as function of average daily flow in Ella and Betsy Cks respectively, and the corresponding ratio of catchment areas. The similarity of the regression gradient to the ratio of the catchment areas reflects the apparent strong dependence of catchment yield on area. The positive constants of the regressions reflects that in summer Ella and Betsy Cks cease flowing because of seepage loss. At other than the lowest flows, the streams exhibited a substantial constancy in their relative response. Fig. 6 shows double-mass plots for the three streams. During the period of active flow of Ella and Betsy Cks the relation appears to be constant while the "flattenings" in the plots are caused by cessation of

flow. The small variations in the slope of the double-mass lines when all streams are flowing indicate that the deep seepage losses vary from year to year. It is concluded that the major difference between the water yield of the streams was the loss of water from Ella and Betsy Cks.

A number of reasons have been considered for such variations in the relative yield. These include: (i) local variations in rainfall causing Clem Ck catchment to receive more than Ella or Betsy Ck. This is rejected because Fig. 4 suggests that Betsy and Clem catchment received similar rainfall. (ii) "deep seepage" out of the catchment which did not pass through the measurement weirs. This could be either at substantial depth or, alternatively, at relatively shallow depths moving downstream. There was no evidence of substantial measurement station "leakage"; however, the weirs were founded on the parent rock which is known to store and transmit groundwater, and it is likely that the steep country would lead to substantial subsurface flow below the cutoff walls of the weirs. It is stressed that given an environment in which water is stored and transmitted in the weathered rock zone, such flow must be regarded as normal and not regarded as a deficiency in the gauging stations. (iii) Suggested possible differences in soil types or depths on the catchments. However, there were no observable differences in the soil or soil depth between the three catchments.

An interesting possibility raised by the persistence of Clem Ck at times of low rainfall, and when other streams had ceased to flow, was whether Clem Ck was somehow "capturing" waters from other streams. We

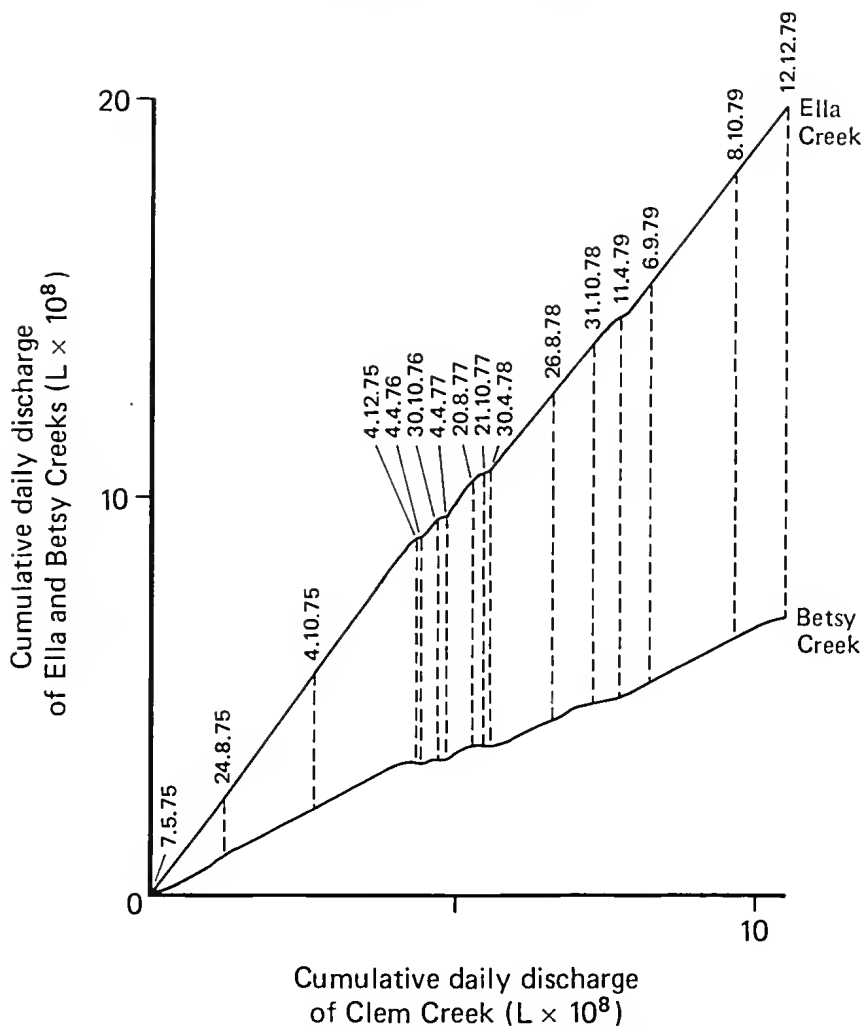


Fig. 6—Double mass plots of Ella and Betsy Creeks with Clem Creek.

could find no hydrograph anomalies which would support such a contention; nor was there any topographic or geologic information which would suggest why such a capture should be occurring. However, in view of the role of the catchment rock material in storing and transmitting groundwater it cannot be ruled out, although our catchments would not be particularly different from most other forested catchments.

Finally, it behoves us to comment on the idealised concept of a "scaled catchment"—i.e. a catchment in which water loss is only by evapotranspiration or by streamflow. If such a thing exists, then Clem Ck must be regarded as the closest approximation in this environment. However, we take the more pessimistic view that in an environment governed by groundwater processes there is no particular reason to suppose that hydrologic gradients should not pass water to adjacent catchments underground; inadequacy of measurement techniques to assess this is a major deficiency.

CATCHMENT WATER BALANCES AT CROPPERS CREEK

Table 3 and Fig. 7 show the annual rainfall and runoff for the three streams at Cropper Ck; below about 700 mm annual rainfall, streamflow would appear to cease. Above this value, the marginal rate of contribution of rainfall to runoff appears to be between 60% and 75%.

Formally, the water balance for a small catchment may be expressed as:

$$T = S + E + I + D + C \quad (1)$$

where T = total precipitation, mm; S = streamflow, mm; E = evapotranspiration, mm; I = interception storage of rainfall, mm; D = deep seepage, mm; and, C = increase of storage of water within the catchment, mm.

In general, only T and S can be measured with any degree of accuracy. By judicious selection of the period over which the water balance is evaluated, C can be

TABLE 3

ANNUAL RAINFALL AT THE PROJECT AREA AND ANNUAL RUNOFF FOR EACH OF THE THREE STREAMS IN THE CROPPER CREEK PROJECT, NORTH-EASTERN VICTORIA

Year	Annual rainfall (mm)	Annual runoff (mm)		
		Clem	Ella	Betsy
1975*	1867	911	764	639
1976	863	109	58	78
1977	1016	149	100	71
1978	1625	463	342	280
1979	1497	627	489	450

* Data only available from mid-May 1975.

zero. Given this, estimates can be made of the catchment loss (E+I+D) by subtraction of observed streamflow from rainfall during the period. The data from Cropper Ck shows two such periods when

estimates can be made: late autumn to late spring (the "wet period") and late spring to late autumn (the "dry period"). The actual period of time varies from year to year but can be broadly categorised by defining the "wet" period as that time during which Betsy Ck is flowing (average 4.4 months per year). The water balance and catchment loss for Clem Ck using this indicator is shown in Table 4. These data show that total evapotranspiration and interception losses are variable with higher losses in "wet" periods, which is possibly due to higher interception losses and the greater availability of soil moisture in this period. The very low "catchment loss" in the summer of 1976 must be regarded as reflecting the moderately severe drought and low water availability at this time.

Fig. 8 shows the monthly ratio of runoff to rainfall (per cent) for the three streams. The catchment yield efficiency is seasonal, with figures of 60% being commonly achieved. Values above 100% reflect the influence of a wet month preceding a dry month, although most storm response is generated within 3 or 4 days of the

TABLE 4

RAINFALL, RUNOFF AND CATCHMENT LOSS* AT CLEM CREEK FOR PERIODS OF HIGH AND LOW SOIL-MOISTURE STATUS, AS INDICATED BY THE PRESENCE OR ABSENCE OF FLOW AT BETSY CREEK, NORTH-EASTERN VICTORIA.

Period	Condition of Betsy Creek	Rainfall (mm)	Clem Creek		
			Runoff (mm)	Runoff Rainfall (%)	Catchment loss* (mm day ⁻¹)
31.7.75 to 22.1.76	Flowing	1303	798	61.2	2.9
23.1.76 to 28.6.76	Dry	163	36	22.1	0.8
29.6.76 to 4.11.76	Flowing	542	45	8.3	3.8
5.11.76 to 28.6.77	Dry	705	34	4.8	2.8
29.6.77 to 23.9.77	Flowing	313	108	34.5	2.4
24.9.77 to 5.7.78	Dry	764	43	5.6	2.5
6.7.78 to 5.1.79	Flowing	987	420	42.6	3.1
6.1.79 to 9.8.79	Dry	531	47	8.9	2.2
10.8.79 to 9.12.79	Flowing	953	569	59.7	3.1

* Catchment loss = Evapotranspiration + Interception + Deep seepage.

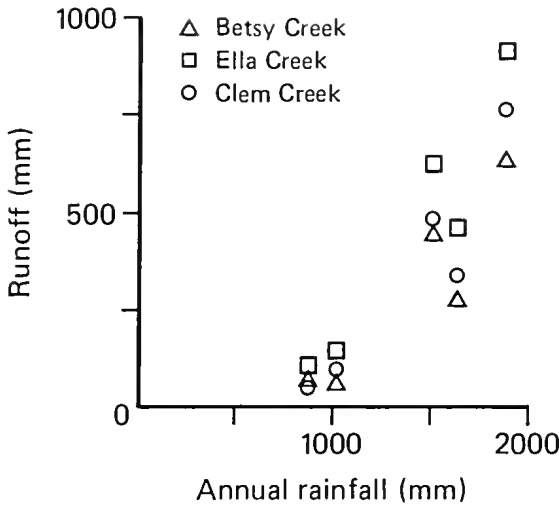


Fig. 7—Annual water yield for the three small streams as a function of annual rainfall.

causal storm rainfall. A general similarity between this ratio and the annual flow variation (Fig. 5) can be seen, reflecting the increased yield from a “wet” catchment compared to a “dry” catchment. The difference in daily water yield (expressed in mm per day) between Clem and Ella and Betsy Cks respectively allows the relative seepage loss for these catchments to be computed. If the arguable assumption is made that Clem Ck is “sealed”

then this gives a measure of the absolute water loss. Fig. 9 shows the estimated relative seepage as a function of time. It is concluded that: (i) Betsy Ck has a substantially greater seepage rate than Ella Ck during the recharge period; and, (ii) An increased rate of seepage is associated with an increased mean monthly streamflow (by comparison with Fig. 5)

Thus, in winter, deep seepage may exceed 2 mm per day while in summer, deep seepage loss is about 0.2 mm per day on Ella and Betsy catchment. The data, combined with the information from Table 4, suggest that deep seepage is similar to transpiration loss in winter but is rather less in summer. The fate of this water is unknown. Nahm (1982) states that the Buffalo Valley is known to be a source of recharge for the Murray Groundwater Basin, and it is possible that this deep seepage recharges these aquifers.

RELATION BETWEEN PERIODIC WATER YIELD IN SMALLER AND LARGER STREAMS

The question of whether a small catchment used for research adequately represents the hydrologic processes governing the behaviour of larger local catchments is both important and difficult. Pilgrim *et al.* (1982) made a detailed examination of the effect of catchment size on runoff relations, and concluded “that while general relationships will exist between small and large catchments no closely defined and simple relationships are likely . . . Without consideration of the factors reviewed here, study of relationships between small and large catchments cannot rise above empiricism and be more than

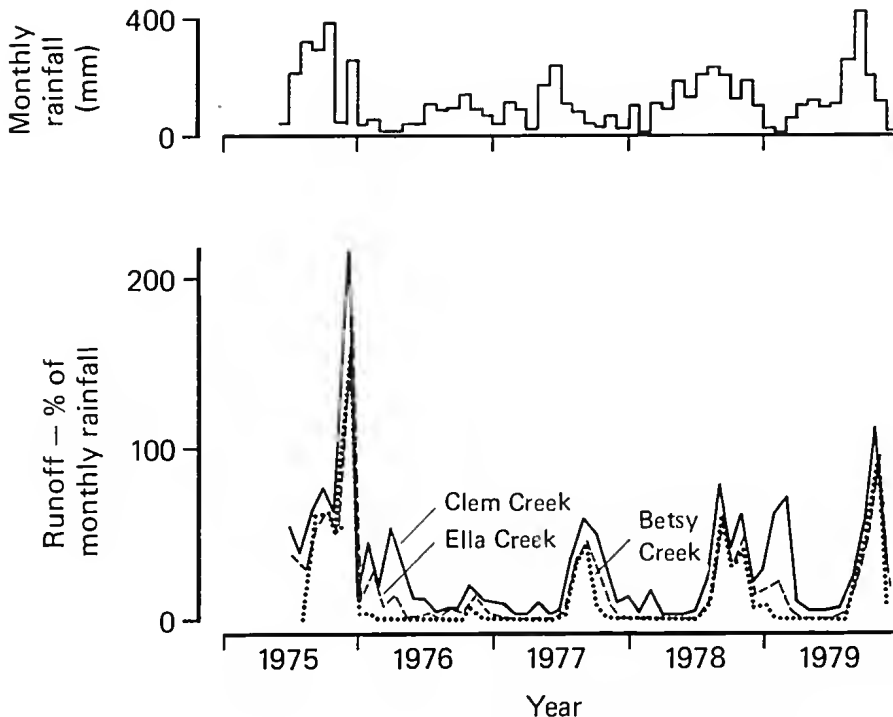


Fig. 8—Monthly ratio of runoff to rainfall for the three small streams.

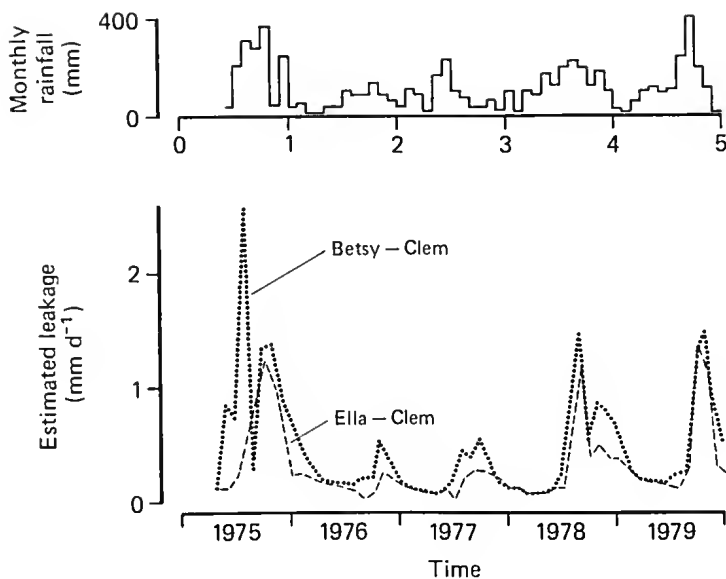


Fig. 9—Estimated seepage loss from Ella and Betsy Creeks as a function of time.

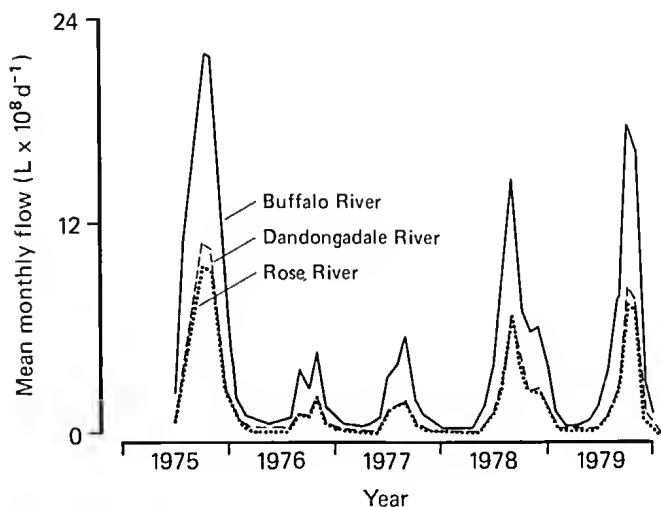


Fig. 10—Mean monthly streamflow of the three larger streams.

site specific". To this end, the study examined whether the Cropper Ck catchments could be regarded as broadly representative of the flow in the larger local streams.

Fig. 10 shows the mean monthly streamflow of the Rose, Dandongadale and Buffalo Rivers; the similarity between these and the mean monthly flow of the smaller streams (Fig. 5) is apparent. Examination of the daily flow in each of these systems, as a function of daily flow in Clem Ck, showed that, overall, the flow in the large and small streams were well-correlated, but that the variance of flow

in each system was about proportional to the mean monthly flow. Thus the flow in the small streams could not be regarded as an accurate predictor of flow in the large streams at periods of higher flow. Fig. 11 shows the double-mass plots between each of the larger rivers and Clem Ck. The results suggest, at best, a constant long-term relation but with significant seasonal variation. It is concluded that the same general pattern of daily and monthly flow variation exists in the two sets of catchments but that variations attributable to unmeasured factors preclude the use of the

TABLE 5
RELATIONSHIPS BETWEEN ANNUAL WATER YIELD AND RUNOFF IN LARGER CATCHMENTS CLOSE TO CROPPER CREEK AND ANNUAL WATER YIELDS AND RUNOFF IN CLEM CREEK

Station	Catchment Area km ²	Area as times Clem Ck. area. (1)	Yield of water as times Clem Ck. yield. (2)	Yield per unit area as a ratio of yield per unit area from Clem Ck*
Rose R.	176	379	288	0.76
Dandongadale R.	181	390	282	0.72
Buffalo R.	425	915	704	0.77
Ella Creek	1.13	2.44	1.87	0.77
Betsy Creek	0.44	0.96	0.68	0.71

* i.e., Col. (2)/Col. (1).

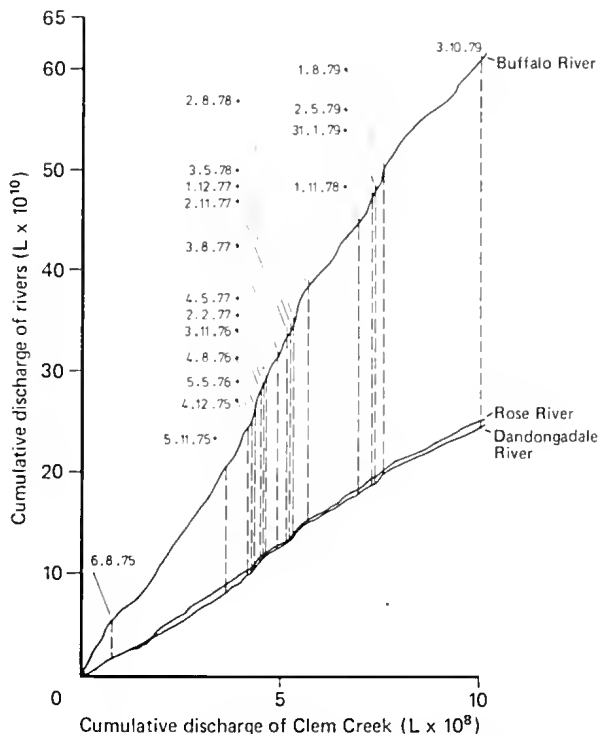


Fig. 11—Double mass plots showing cumulative flow in the larger rivers as a function of the cumulative flow in Clem Creek.

smaller streams as highly-accurate predictors of the larger streams. Major factors would be rainfall variations, the presence of snow, and the size and shape of the catchments.

Table 5 shows the water yield per unit area of all catchments in relation to the yield per unit area from the Clem Ck catchment. The results indicate the larger catchments produce an overall average quite similar to that produced by Ella and Betsy Cks. However, the rainfall gradients

across the larger catchments means that use of Cropper Ck rainfall data probably underestimates total rainfall on the catchments and that a crude water balance cannot be computed. Given the imperfections of routine gauging measurements of larger rivers, the water outputs per unit area from the catchments are surprisingly close to those of Ella and Betsy Cks. It is concluded that water yield and general response from the streams at Cropper Ck are broadly representative of the larger streams, although Clem Ck is probably closer to the concept of the "sealed catchment" than the average stream in this area. Achieving a higher level of accuracy in such studies is not feasible without installation of a hydrometeorological network in this region.

ACKNOWLEDGEMENTS

Many Officers of both the (then) State Rivers and Water Supply Commission and the (then) Forests Commission Victoria assisted. Particular thanks are due to Mr Leon Stephens who bore the brunt of onerous servicing of equipment. Ms Rae Moran and officers of the MMBW assisted with data processing and critical comment.

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ALATALEBERIS NEW GENUS (CRUSTACEA, OSTRACODA) FROM THE TERTIARY OF VICTORIA AND SOUTH AUSTRALIA

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ABSTRACT: A new trachyleberidid ostracode genus, *Alataleberis*, is described from the Tertiary of southeastern Australia for the new species *A. johannae* (type species), *A. robusta*, and *A. miocenica*, and the new species and subspecies *A. ornithopetrae ornithopetrae* and *A. ornithopetrae willungae*. Our new genus is compared with specimens of *Alatacythere* from the Gulf Coast of the United States and with *Pterygocythereis* from the Atlantic/Mediterranean. Its stratigraphic usefulness is indicated.

The Tertiary Ostracoda of southeastern Australia remain poorly known (McKenzie 1974) although recent work in the Miocene of Victoria suggests that the situation is about to ameliorate (McKenzie & Neil 1983, Whatley & Downing 1983, McKenzie & Peypouquet 1984). During a broader study of several Miocene sequences in Victoria, one of us (M.T.W.) came across a new taxon with apparent affinities to the genus *Alatacythere* from the Gulf Coast Tertiary of the United States. Discussion with the senior author led to the consensus that this species represented a new generic category (n. gen. D. aff. *Alatacythere* of McKenzie, in Cooper 1979). The senior author had already identified several species of the new taxon: in the Eocene of Victoria (2 species); and, in the Eocene-Oligocene of South Australia and Victoria (1 species with 2 subspecies). The Miocene species is a fourth member of this group. As far as we are aware, there are no Pliocene or Quaternary species, nor are any species earlier than the (P16) Eocene taxa known to us. The general localities are illustrated in Fig. 1; more detailed locality data are provided with the species descriptions.

As the senior author's collections include reference material from the United States Tertiary, it was convenient to compare our new genus with the type and related species of *Alatacythere*. We also compare it with the well known Atlantic and Mediterranean genus *Pterygocythereis*.

The conventions RV=right valve, LV=left valve, L=length, H=height and B=breadth are used throughout. Types are stored in the palaeontological collections of the Museum of Victoria under Register Numbers NMV P109896-P109901, P111421-P111429 and P111790-P111792.

SYSTEMATIC PALAEOLOGY

Family TRACHYLEBERIDIDAE Sylvester Bradley 1948
Subfamily TRACHYLEBERIDINAE Sylvester Bradley 1948

? Tribe PTERYGOCYTHEIDEINI Puri 1957

Genus *Alataleberis* gen. nov.

TYPE SPECIES: *Alataleberis johannae* sp. nov.

ETYMOLOGY: *Alata*-(L)=winged; and suffix *-leberis* (Gk)=sloughed skin, a reference to the fact that

Ostracoda, like other crustaceans, are eedysists. The genus is feminine.

DIAGNOSIS: A new pterygoeotherideid genus with a carapace which features alate ventral ridges usually perforated along their length, non-alate dorsal ridges and secondary yoke-like, areuate posterior ridges, the valve surfaces otherwise being smooth. Minor features of the ornament include anteromarginal spinules and strong dorsal and posteroventral spines. Inner lamellae are moderately broad with no or only very small vestibules; marginal pore canals are flexuous, often branched and fairly numerous; normal pore canals are sieve-type, eelated and scattered; central muscle scars comprise 4 adductors, a V-shaped frontal scar and a mandibular scar; the hinge is hemiamphidont. The subcentral tubercle may be well (*A. robusta*) or poorly developed but an eye tubercle is distinct in all species; as is sexual dimorphism.

REMARKS: The new genus has been compared previously (McKenzie 1974, McKenzie, in Cooper 1979) with *Pterygocythereis* and *Alatacythere*. Both these genera were formerly placed in the family Brachyeytheridae (Moore 1961) but were transferred to Trachyleberididae in a more recent revision (Hartmann & Puri 1974). The type species of *Pterygocythereis* Blake 1933 is the North Atlantic and Mediterranean taxon *P. jonesi* (Baird 1850). We illustrate this species in Fig. 4 F, J and Fig. 5 E, F, G, I, J along with *P. ceratoptera* (Bosquet 1852) in Fig. 5 H, both specimens coming from the senior author's Bay of Naples collection. Our new genus resembles *Pterygocythereis* in that the shell surface is smooth and the margins are spinose in both genera. The differences, however, are striking. Anteromarginally, *Alataleberis* bears spinules rather than broad flat-topped "spines" as in *Pterygocythereis*; dorsally, the Atlantic/Mediterranean taxon bears a marginal row of large spines rather than a few thorn-like spines on a low dorsal ridge as in *Alataleberis*; and the ventral ridge in *Pterygocythereis* carries a row of separate large spines which increase in length posteriorly (the final spine being about twice as long as its neighbours) whereas in *Alataleberis* the ridge itself increases in height posteriorly, terminating in a

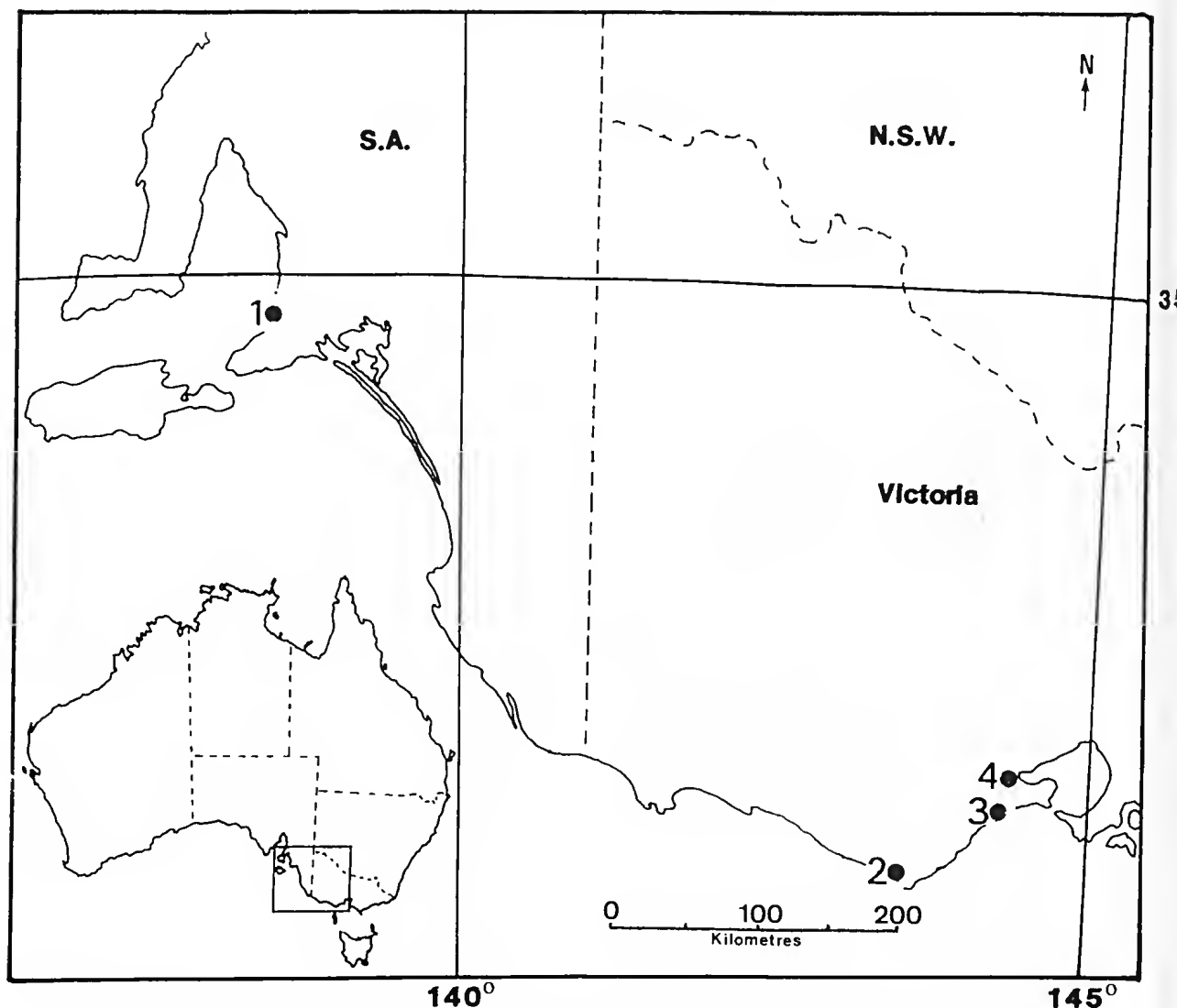


Fig. 1—Locality diagram. 1, Maslin Bay/Aldinga Bay. 2, Browns Creek/Castle Cove. 3, Torquay. 4, Geelong/Fyansford.

single stout spine. Therefore, in dorsal view *Alataleberis* is regularly subhastate with the greatest breadth posteromedial (Fig. 2 B, G, H) while in *Pterygocythereis* the profile is subelliptical (discounting the spines)—well illustrated in Bonaduce, Ciampo and Masoli (1975, Plate 29, Fig. 3). Posteriorly, *Alataleberis* is subacuminat in all species (except the LV of *A. robusta*) whereas *P. jonesi* is rounded posteriorly (although *P. ceratoptera* is subacuminat). The eye tubercle is prominent and nearly spherical in *Pterygocythereis* but somewhat smaller in *Alataleberis*. Finally, there is a slight difference in hinge-ment, with *Pterygocythereis* having a smooth posterior RV tooth while in *Alataleberis* this tooth is divided into two elements by a small furrow, the more anterior element being larger (Fig. 4 I). Another species of *Pterygocythereis* from the Alum Bluff Chipola Miocene

of Florida, U.S.A. is also illustrated (Fig. 5 A, B) for comparison.

The genus *Alatacythere* Murray & Hussey 1942 was described from the Vicksburg (Oligocene) of the Gulf Coast region of the United States where it ranges from Late Cretaceous to Neogene. Specimens in the senior author's collection from the type horizon in the Byram Marl, Mississippi, are A-I juvenile females. We illustrate instead, therefore, an adult male and female from the Mint Spring Oligocene, south of Hiwance, Missouri, collected by the late Prof. H. V. Howe from a roadcut on U.S. Highway 45 (Fig. 4 G, Fig. 5 K, L, M). This taxon seems very close to the type species *A. ivani* Howe 1951 (*nom. nov. for Cythereis (Pterygocythereis?) alexanderi* Howe & Law 1936—the designated type species of *Alatacythere*—which is a junior homonym) except that it

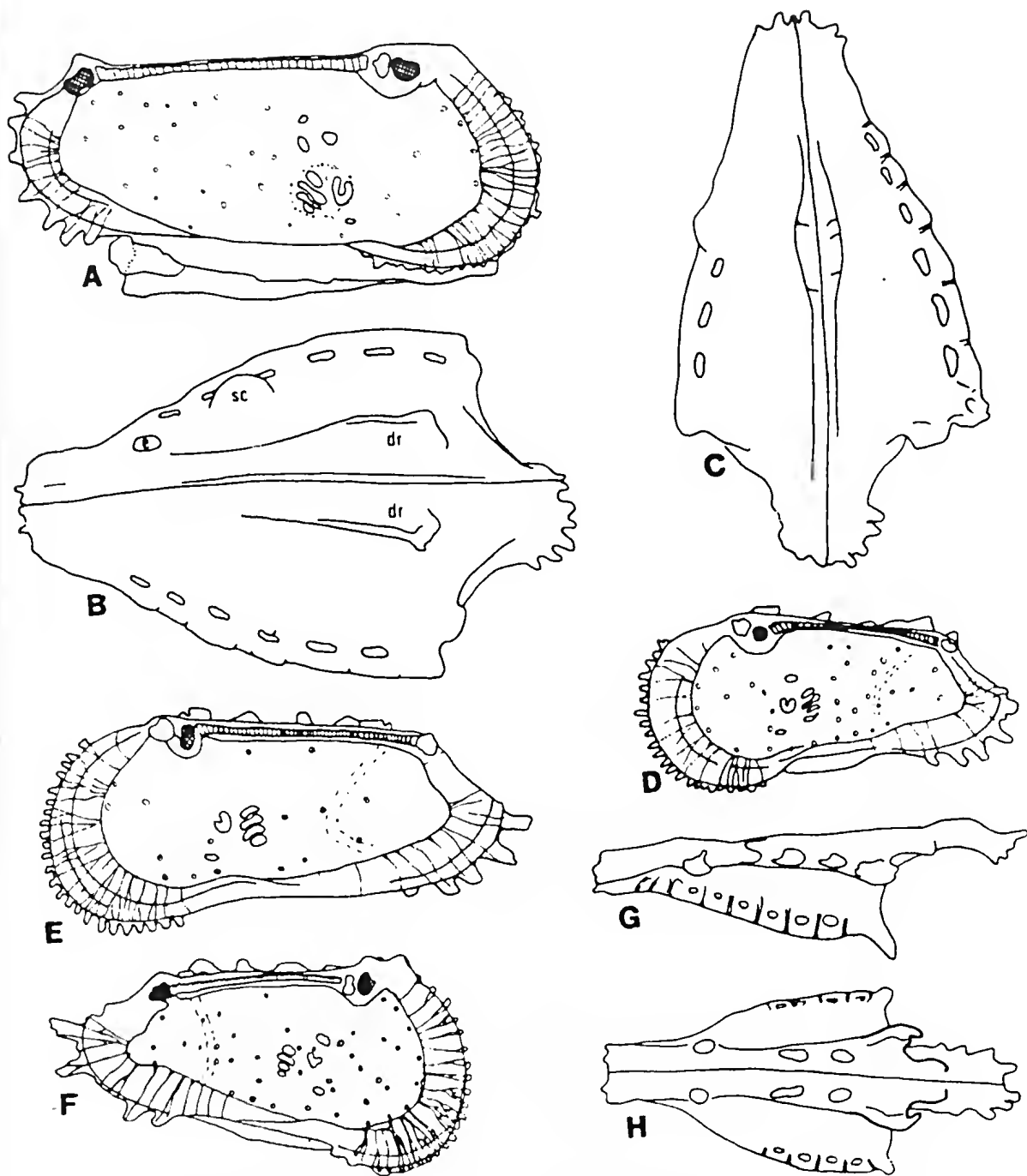


Fig. 2—A, *Alataleberis robusta* sp. nov., male, internal, L.V., $\times 75$. B, *Alataleberis robusta* sp. nov., male, dorsal, $\times 75$. C, *Alataleberis robusta* sp. nov., male, ventral, $\times 75$. D, *Alataleberis miocenica* sp. nov., female, internal, R.V., $\times 75$. E, *Alataleberis johannae* sp. nov., male, R.V., $\times 75$. F, *Alataleberis ornithopetrae ornithopetrae* subsp. nov., female, internal, L.V., $\times 75$. G, *Alataleberis ornithopetrae ornithopetrae* subsp. nov., female, dorsal, L.V., $\times 75$. H, *Alataleberis ornithopetrae willungae* subsp. nov., female, dorsal, $\times 75$.

is more elongate. In *Alatacythere*, anteromarginal spines are broad and flat-topped, unlike the anteromarginal spinules of *Alataleberis*; dorsal spines are few, broad and fragile, especially anterodorsally, in *Alatacythere* (Howe & Law 1936, Plate IV, Fig. 23)—the anterodorsal spine is damaged in our figured specimens (Fig. 5 K, L, M)—whereas *Alataleberis* has a low dorsal ridge terminating in a posterior spine (all species) and sometimes having 2-3 other short thorn-like spines. The strong ventral ridge which provides the generic prefix for both taxa is reinforced by buttressing along its length in both *Alatacythere* and *Alataleberis*, but is not perforated in any species of *Alatacythere* known to us whereas it is distinctly perforated in most *Alataleberis* species, especially those in which this ridge is most notably developed (*A. robusta* and *A. ornithopetrae*). In *Alataleberis*, the dorsal and ventral ridges are yoked together by an arcuate subridge (poorly defined in *A. robusta*) but there is no trace of this subsidiary feature in *Alatacythere*, doubtless because the latter lacks a distinct dorsal ridge. Eye tubercles are small and weak in *Alatacythere* but always distinct in the new genus. In dorsal view, both genera are subhastate with the ventral alar extensions making for a more extremely "winged" profile in most *Alatacythere* species although a few Neogene taxa with low ventral ridges have been described (Fig. 4 G, Fig. 5 K, L, M). *Alatacythere* sp. from the Upper Oligocene Chickasawhay Limestone, Florida, U.S.A. is also illustrated (Fig. 5 C, D) for comparison. Hartmann and Puri (1974) also designated the genera *Pterygocythere* Hill 1954, and *Incongruella* Ruggieri 1958 with its subgenera *Incongruella* Ruggieri 1958 and *Lixouria* Uliczny 1969 as belonging in Pterygocytherideidini. Of these taxa, *Lixouria* was based on a misidentified type species and the latest reviewer (Uffenorde 1981) considers it indeterminate to subfamily. The taxon illustrated as "*Lixouria*" *unicostulata* (Kuiper 1918) s.l. by Uffenorde (1981, Plate 2, figs 9-10) seems close to such non-ptyergocytherideidine genera as *Ruggieria* Keij 1957 and *Keijella* Ruggieri 1967. Sissingh (1973) established a new genus, *Carinivalva* Sissingh 1973 for taxa placed in *Lixouria* by Uliczny and, later, himself (Sissingh 1972). All these taxa clearly differ from *Alataleberis*. Firstly,

Pterygocythere has a well-developed, strongly-convex, dorsal flange above the hinge line that is diagnostic and is used to distinguish it from *Alatacythere* which otherwise it closely resembles; no species of *Alataleberis* has this feature. Next, *Incongruella* and *Carinivalva* both have prominent ventral carinate (or keel-like) ridges and their general shape is similar to the well known European Cainozoic genus *Bosquetina* Keij 1957; all three genera, apart from their generally different shape to *Alataleberis*, lack the dorsal ridge which is a feature of the new taxon.

Our questionable reference of *Alataleberis* to Pterygocytherideidini is based on the fact that Hartmann and Puri (1974, p. 38) define the tribe as comprising alate trachyleberidids with simple normal pores whereas all species of *Alataleberis* have sieve-type normal pores, although difficult to illustrate (Fig. 4 H). Since it is now known that both sieve-type and simple normal pore canals can occur on the same trachyleberidid species, this criterion has lost the taxonomic weight it formerly had in determining relationships within the family. Nevertheless, our uncertainty remains and we recognise that future workers may decide that *Alataleberis* is convergent towards Pterygocytherideidini rather than belonging in the tribe.

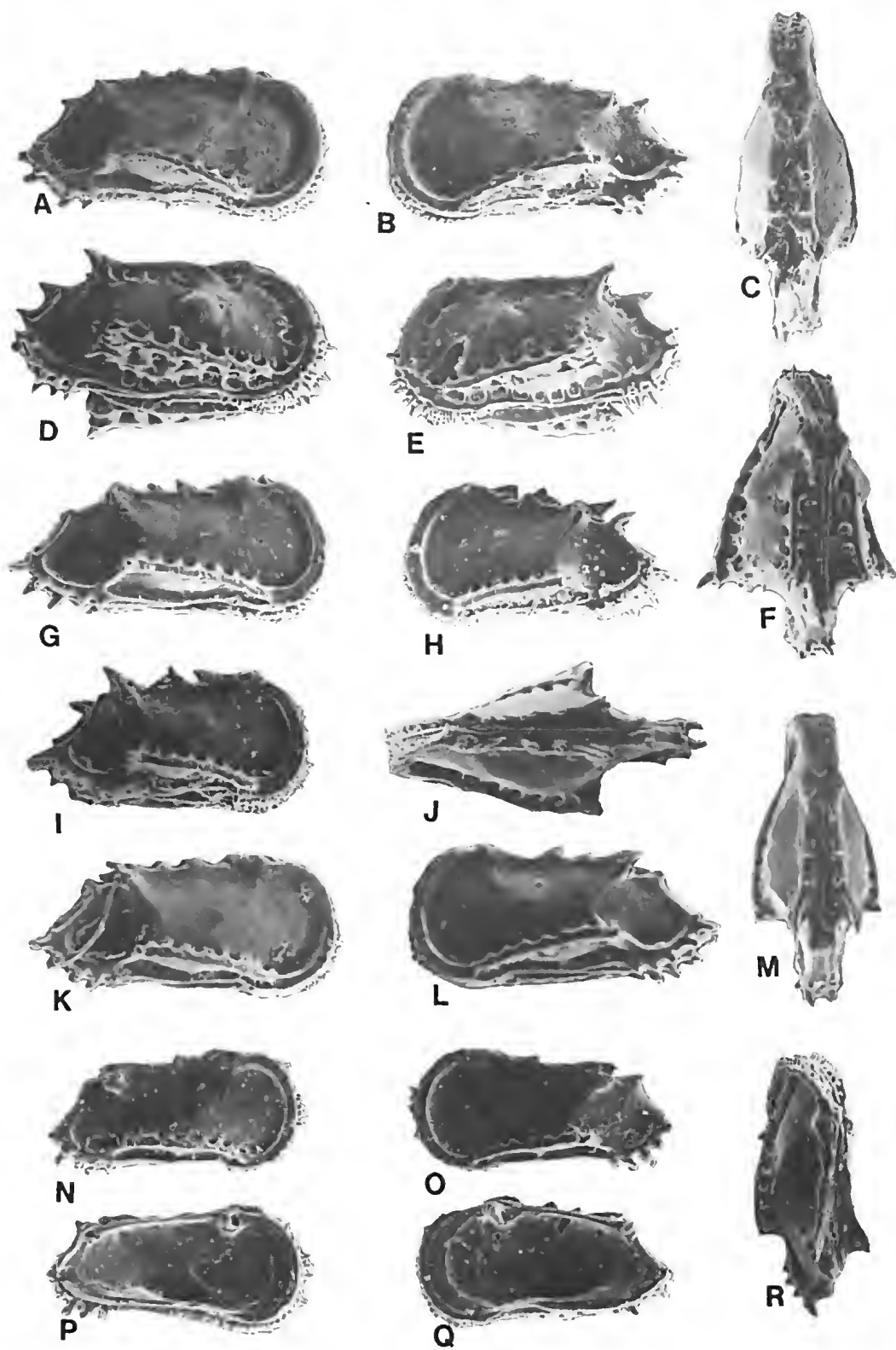
A similar uncertainty is recorded for the only taxon known to us which may be ancestral to our new genus, that is *Ponticulocythere* Dingle 1981, described from the Maastrichtian of southeast Africa (Dingle 1981) and yet to be recognised from Australia (Bate 1972, Neale 1975). Like *Alataleberis*, *Ponticulocythere* has dorsal and ventral ridges and is compared by its author with *Bosquetina* and *Pterygocythereis*. But *Ponticulocythere* differs in that its hinge is more primitive, being entomodont rather than amphidont, and because both its dorsal and its ventral ridge are perforate and buttressed—in *Alataleberis* only the ventral ridge is perforate and buttressed in most species (except *A. robusta* in which the dorsal ridge also is buttressed but not perforate).

Alataleberis johannae sp. nov.

Figs. 2 E, 3 A, B, C

ETYMOLOGY: *johannae* = locality name from the Johanna River area in Victoria, where the type locality is exposed along the coast.

Fig. 3—A, *Alataleberis johannae* sp. nov., paratype, male, lateral, R.V., $\times 45$. NMV Reg. No. P111792. B, *Alataleberis johannae* sp. nov., paratype, male, lateral, L.V., $\times 45$. NMV Reg. No. P111792. C, *Alataleberis johannae* sp. nov., paratype, male, dorsal, $\times 47$. NMV Reg. No. P111792. D, *Alataleberis robusta* sp. nov., paratype, female, lateral, R.V., $\times 45$. NMV Reg. No. 111424. E, *Alataleberis robusta* sp. nov., paratype, female, lateral, L.V., $\times 45$. NMV Reg. No. P111424. F, *Alataleberis robusta* sp. nov., paratype, female, dorsal, $\times 43$. NMV Reg. No. P111424. G, *Alataleberis ornithopetrae ornithopetrae* subsp. nov., paratype, male, lateral, R.V., $\times 45$. NMV Reg. No. P111791. H, *Alataleberis ornithopetrae ornithopetrae* subsp. nov., paratype, female, lateral, L.V., $\times 43$. NMV Reg. No. P111790. I, *Alataleberis ornithopetrae ornithopetrae* subsp. nov., paratype, female, lateral, R.V., $\times 44$. NMV Reg. No. 111790. J, *Alataleberis ornithopetrae ornithopetrae* subsp. nov., paratype, male, dorsal, $\times 46$. NMV Reg. No. P111791. K, *Alataleberis ornithopetrae willungae* subsp. nov., paratype, male, lateral, R.V., $\times 45$. NMV Reg. No. P111429. L, *Alataleberis ornithopetrae willungae* subsp. nov., paratype, male, lateral, L.V., $\times 45$. NMV Reg. No. P111429. M, *Alataleberis ornithopetrae willungae* subsp. nov., paratype, male, dorsal, $\times 42$. NMV Reg. No. P111429. N, *Alataleberis miocenica* sp. nov., holotype, male, lateral, R.V., $\times 45$. NMV Reg. No. P111427. O, *Alataleberis miocenica* sp. nov., holotype, male, lateral, L.V., $\times 45$. NMV Reg. No. P111427. P, *Alataleberis miocenica* sp. nov., paratype, male, lateral (internal), L.V., $\times 45$. NMV Reg. No. P111422. Q, *Alataleberis miocenica* sp. nov., paratype, female, lateral (internal), R.V., $\times 46$. NMV Reg. No. P111423. R, *Alataleberis miocenica* sp. nov., holotype, male, dorsal, $\times 45$. NMV Reg. No. P111427.



MATERIAL AND DISTRIBUTION: Numerous carapaces and valves from several horizons in the sections exposed at Browns Creek and Castle Cove, Victoria.

DESCRIPTION: Carapace medium-large (length 0.90-0.97 mm); subrectangular in lateral view with a smooth shell surface and weakly developed subcentral tubercle; anterior broadly rounded and adorned marginally with numerous spinules; posterior subacuminate (or subcaudate) in both LV and RV, carrying about 5 large posteroventral spines; dorsal margin straight, sloping backwards slightly from front to rear; ventral margin mostly straight but weakly inflexed anteromedially in the mouth region; ornament of ridges and thorn-like spines. The dorsal ridge extends posteriorly from the eye tubercle, carries 2 thorn-like spines and terminates in a stout spine; behind and below this ridge there is another thorn-like spine at the posterodorsal corner of the valve; anteriorly, a marginal ridge commences in front of the eye tubercle and follows the margin until it meets the ventral ridge in the anteroventral region. The ventral ridge is strong and is more elevated in the rear than the dorsal ridge; it is strengthened along its length by buttresses and ends in a broad-based, powerful short spine. An arcuate subridge yokes the dorsal and ventral ridges in the posterior region of each valve. Greatest height is in the eye tubercle plane and equals about half the length. In dorsal view, the carapace is subhastate, with the greatest breadth posteromedial and about 37% of the length. *Internally*, the inner lamellae are moderately broad, with a regular line of concrescence and, possibly, a small posterior vestibule (Fig. 2 E); marginal pore canals are more numerous anteriorly than posteroventrally, flexuous and often branched; normal pore canals are sieve-type, celated and irregularly scattered; the central muscle scars comprise 4 adductors, a V-shaped frontal scar and a ventral mandibular scar; the hinge is amphidont-hemiamphidont with a weakly crenulate posterior tooth in the RV and a crenulate median element. Eye tubercle distinct. Sexual dimorphism, females shorter and higher than males.

DIMENSIONS (mm): Holotype, adult male, NMV Reg. No. P109896, L=0.96, H=0.44, B=0.36. Paratype, adult female, NMV Reg. No. P109897, L=0.92, H=0.44, B=0.34. Paratype, adult male, NMV Reg. No. P11792, L=0.95, H=0.44, B=0.35.

TYPE LOCALITY: Browns Creek Clays above the *Notostraea* Greensand horizon, at the Browns Creek coastal section near Johanna River, Victoria.

REMARKS: The type species differs from others in the genus in that the ventral ridge is only indistinctly perforated along its length.

GEOLOGICAL AGE: Aldingan-Janjukian, P 16-18 (Late Eocene-earliest Oligocene).

Alataleberis robusta sp. nov.

Figs 2A, B, C, 3D, E, F

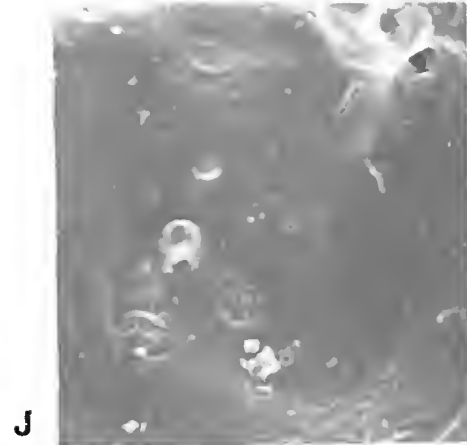
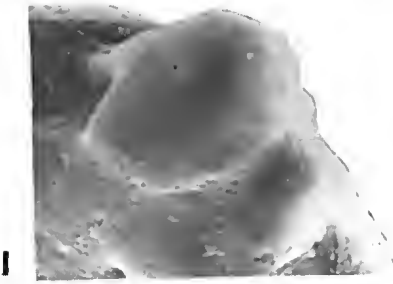
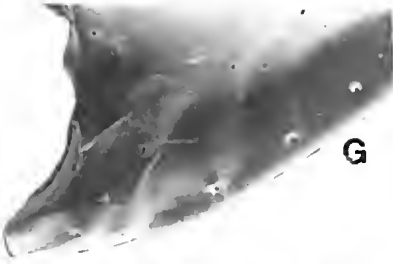
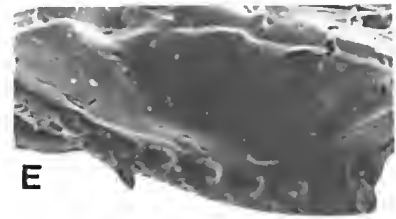
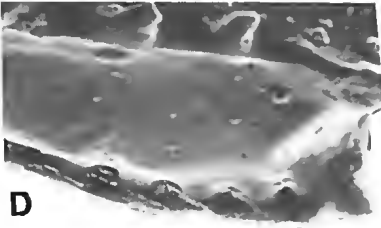
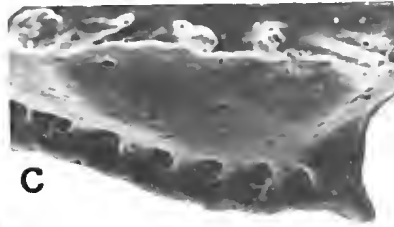
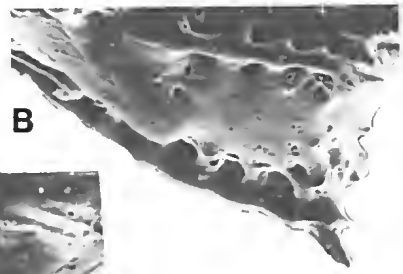
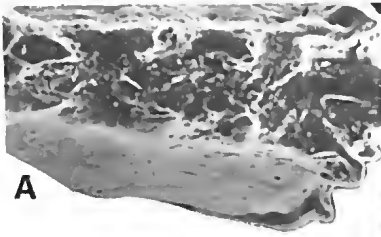
1974 *Alatacythere* sp. BCC 6 McKenzie, Plate 2, Fig. 6.

ETYMOLOGY: *robusta* (L)=robust.

MATERIAL AND DISTRIBUTION: Several carapaces and valves from the sections at Browns Creek and Castle Cove, Victoria.

DESCRIPTION: An *Alataleberis* of relatively large size (length 0.90-1.10 mm), subrectangular in lateral view with a smooth shell surface and distinct subcentral tubercle; anterior broadly rounded and adorned marginally with numerous spinules; posterior less broadly rounded in the LV and subcaudate in the RV, carrying several (5-8) strong marginal spines; dorsal margin straight, sloping backwards slightly; ventral margin mostly straight but inflexed anteromedially in the mouth region; ornament of ridges and spines. The dorsal ridge is more prominent than in other species and buttressed, ending in a stout spine; anteriorly a ridge follows the margin to the anteroventral corner where it meets the ventral ridge. The ventral ridge is very strong and inflated characteristically for the genus. The ridge increases markedly in height from front to rear, is strengthened by 6 buttressing struts, between which are perforations (about 6 overall) and ends in a powerful spine which carries 1-2 subsidiary spinules posteriorly. A yoking subridge is indistinctly defined on some specimens. Greatest height is in the eye tubercle plane and equals half the length. In dorsal view, the carapace is robustly subhastate, with the greatest breadth posteromedially and about two-thirds the length. *Internally*, the lamellae are moderately broad; line of concrescence regular; possibly a small posteroventral vestibule occurs; marginal pore canals are numerous, flexuous and usually branched; normal pore canals sieve-type and scattered; central muscle scars comprise 4 adductors, a V-shaped frontal scar and an anteroventral mandibular scar; dorsal muscle scars include at least 3 prominent scars above the central scar field of which 2 are mandibular muscle attachment scars; hinge amphidont-hemiamphidont, similar to *A. johannae*. Eye tubercle distinct. Sexual dimorphism, females shorter and higher than males.

Fig. 4—A, *Alataleberis johannae* sp. nov., paratype, dorsal, L.V., ala enlargement, $\times 90$. NMV Reg. No. P111792. B, *Alataleberis robusta* sp. nov., paratype, dorsal, L.V., ala enlargement, $\times 90$. NMV Reg. No. P111424. C, *Alataleberis ornithopetrae ornithopetrae* sp. nov., paratype, dorsal, L.V., ala enlargement, $\times 90$. NMV Reg. No. P111791. D, *Alataleberis ornithopetrae willungae* sp. nov., paratype, dorsal, L.V., ala enlargement, $\times 90$. NMV Reg. No. P111429. E, *Alataleberis niocenica* sp. nov., holotype, dorsal, L.V., ala enlargement, $\times 90$. NMV Reg. No. P111427. F, *Pterygocythereis jonesi* (Baird, 1850), dorsal, L.V., ala enlargement, $\times 85$. NMV Reg. No. P111796. G, *Alatacythere* sp. 2 (specimen from the Mint Spring Oligocene, U.S.A.) dorsal, R.V., ala enlargement, $\times 95$. NMV Reg. No. P111800. H, *Alataleberis ornithopetrae ornithopetrae* subsp. nov., paratype, sieve-type normal pore, $\times 7,650$. NMV Reg. No. P111791. I, *Alataleberis niocenica* sp. nov., paratype, posterior, R.V. tooth of hingement, $\times 700$. NMV reg. No. P111423. J, *Pterygocythereis jonesi* (Baird, 1850), central muscle scar pattern, $\times 350$. NMV Reg. No. P111797.



DIMENSIONS (mm): Holotype, adult female, NMV Reg. No. P109900, $L=0.90$, $H=0.46$, $B=0.56$. Paratype, adult male RV, NMV Reg. No. P109901, $L=0.96$, $H=0.48$. Paratype, adult female, NMV Reg. No. P111424, $L=0.90$, $H=0.45$, $B=0.56$.

TYPE LOCALITY: Browns Creek Clays at the coastal section near Browns Creek, Johanna River district, Victoria. The species ranges from about 8 m below the *Notostraea* Greensand member of the Browns Creek Clays to the basal Castle Cove Limestone at Castle Cove, Victoria.

REMARKS: The species is differentiated from the other *Alataleberis* species by its more strongly alate appearance (especially in dorsal view), prominent and buttressed dorsal ridge and well-developed subcentral tubercle.

GEOLOGICAL AGE: Aldingan, P 16-17 (Late Eocene).

Alataleberis ornithopetrae sp. nov.

A. ornithopetrae ornithopetrae subsp. nov.

Figs 2F, G, 3G, H, I, J

1974 *Alatacythere* sp. McKenzie, Plate 2, Fig. 7.

ETYMOLOGY: *ornitho-* (Gk)=bird; and suffix *-petrae* (L)=rock; from Bird Rock, near Torquay, Victoria, and type locality.

MATERIAL AND DISTRIBUTION: A number of valves and carapaces from the Torquay district coastal section, Victoria, between Bells Headland and Bird Rock in the Jan Juc Formation and Point Addis Limestone of the Torquay Group.

DESCRIPTION: An *Alataleberis* with features intermediate between *A. johannae* and *A. robusta* in that it is almost as broad as the latter and has about 6 perforations in the expanded ventral ridge; but resembling the type species in having a weakly-developed subcentral tubercle and non-buttressed dorsal ridge. Further, the thorn-like dorsal ridge spines are more prominent than in other *Alataleberis* and there is also a strong posterodorsal spine beyond and below the end of the dorsal ridge. The eye tubercle is distinct. Sexual dimorphism present and similar to other species of the genus.

DIMENSIONS (mm): Holotype, adult male, NMV Reg. No. P109898, $L=0.96$, $H=0.42$, $B=0.52$. Paratype, adult female, NMV Reg. No. P109899, $L=0.90$, $H=0.44$, $B=0.52$. Paratype, adult male, NMV Reg. No. P111791, $L=0.97$, $H=0.42$, $B=0.52$. Paratype, adult female, NMV Reg. No. P111790, $L=0.90$, $H=0.44$, $B=0.52$.

TYPE LOCALITY: Jan Juc Formation at Bird Rock, near Torquay, Victoria, 1 m above the *Chione* bed.

GEOLOGICAL AGE: Janjukian, P 18-20? (Oligocene).

Alataleberis ornithopetrae willunga subsp. nov.

Figs 2H, 3K, L, M

ETYMOLOGY: *willunga*=locality name from the Willunga Embayment, South Australia where this subspecies typically occurs.

MATERIAL AND DISTRIBUTION: Numerous valves and carapaces from the Maslin Bay/Aldinga Bay coastal section, in the Tortachilla Limestone and in the Aldingan

Member and Ruwaring Member of the Port Willunga Formation.

DESCRIPTION: This subspecies is very like *A. o. ornithopetrae* except that all specimens are less broad in dorsal view. Further, the terminal spine of the dorsal ridge is strongly recurved, a feature which is lacking in *A. o. ornithopetrae*. Since the ranges of the two taxa are allopatric we feel justified in proposing a new subspecific name.

DIMENSIONS (mm): Holotype, adult female, NMV Reg. No. P111428, $L=0.90$, $H=0.45$. Paratype, adult male, NMV Reg. No. P111429, $L=0.96$, $H=0.43$, $B=0.49$. Paratype, adult male, NMV Reg. No. P111421, $L=0.90$, $H=0.43$, $B=0.40$.

TYPE LOCALITY: Ruwaring Member of the Port Willunga Formation, from the coastal section near the old jetty, Aldinga Bay, South Australia.

GEOLOGICAL AGE: Aldingan=Longfordian, P16-N6 (Late Eocene-Early Miocene).

Alataleberis miocenica sp. nov.

Figs 2D, 3N, O, P, Q, R

ETYMOLOGY: *miocenica* (L)=Miocene, for the geological age of this taxon.

MATERIAL AND DISTRIBUTION: A number of valves and carapaces from both limestone and marly facies in the Miocene formations of the Fyansford district, Victoria; the Fishing Point Marl of the Aire River district, Victoria; the Sherwood Marl of the Western Port Basin, Victoria; and at Clifton Bank near Hamilton, Victoria.

DESCRIPTION: An *Alataleberis* differentiated by its smaller size from all other species in the genus; from *A. robusta* and *A. ornithopetrae* by its more slender dorsal profile (similar to *A. johannae*); from *A. johannae* by a less strongly arcuate yoking subridge and by the occurrence (in *miocenica*) of 2 small perforations in the anterior part of the ventral ridge. The eye tubercle appears to be smaller than in other species of *Alataleberis* but is nonetheless distinct. Sexual dimorphism present, following the established pattern for this genus.

DIMENSIONS (mm): Holotype, adult male, NMV Reg. No. P111427, $L=0.80$, $H=0.36$, $B=0.32$. Paratype, adult female, NMV Reg. No. P111426, $L=0.76$, $H=0.38$, $B=0.32$. Paratype, adult male LV, NMV Reg. No. P111425, $L=0.80$, $H=0.36$. Paratype, adult male, NMV Reg. No. P111422, $L=0.79$, $H=0.35$. Paratype, adult female, NMV Reg. No. P111423, $L=0.79$, $H=0.40$.

TYPE LOCALITY: Fyansford Clay in the Batesford Limestone quarry, near the base of the upper bench, Fyansford, Victoria.

GEOLOGICAL AGE: Longfordian-Balcombian, N 6-9, (Early-early Middle Miocene).

DISCUSSION ON STRATIGRAPHIC UTILITY

Our investigation of the diversity in *Alataleberis* has covered a wide range of Tertiary formations and facies, notably the classic Maslin Bay/Aldinga Bay section, near Port Willunga and some Willunga Embayment boreholes, South Australia; plus the full extent of Tertiary outcrops in Victoria, from the Port Campbell and

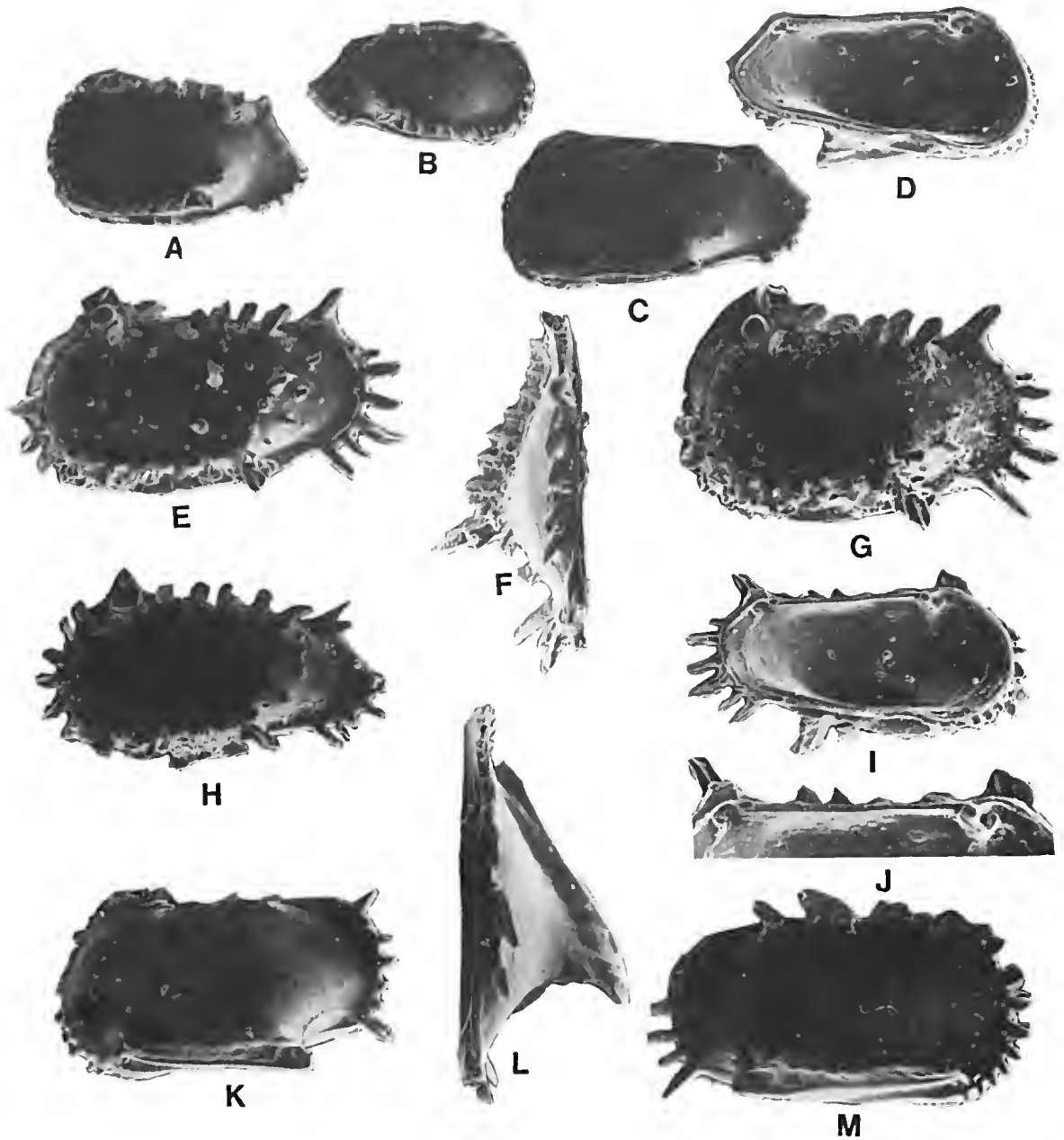


Fig. 5—A, *Pterygocythereis* sp. (from Alum Bluff Chipola Miocene, U.S.A.) lateral L.V., $\times 45$. NMV Reg. No. P111794. B, *Pterygocythereis* sp. (same as above), lateral, R.V., $\times 45$. NMV Reg. No. P111793. C, *Alatacythere* sp. 1 (from Chickasawhay Lst, U.S.A.), lateral, L.V., $\times 45$. NMV Reg. No. P111795. D, *Alatacythere* sp. 1, L.V., $\times 45$. NMV Reg. No. P111795. E, *Pterygocythereis jonesi* (Baird, 1850), lateral, L.V., $\times 50$. NMV Reg. No. P111797. F, *Pterygocythereis jonesi* (Baird, 1850), dorsal, L.V., $\times 50$. NMV Reg. No. P111796. G, *Pterygocythereis jonesi* (Baird, 1850), lateral, L.V., $\times 50$. NMV Reg. No. P111796. H, *Pterygocythereis ceratoptera* (Bosquet, 1852), lateral, L.V., $\times 50$. NMV Reg. No. P111798. I, *Pterygocythereis jonesi* (Baird, 1850), lateral, L.V., $\times 45$. NMV Reg. No. P111797. J, *Pterygocythereis jonesi* (Baird, 1850), hinge enlargement, $\times 60$. NMV Reg. No. P111797. K, *Alatacythere* sp. 2 (specimen from Mine Spring Oligocene, U.S.A.) male, lateral, L.V., $\times 45$. NMV Reg. No. P111799. L, *Alatacythere* sp. 2, female, dorsal, R.V., $\times 50$. NMV Reg. No. P111800. M, *Alatacythere* sp. 2, female, lateral, R.V., $\times 50$. NMV Reg. No. P111800.

Hamilton districts eastwards to Lakes Entrance and Orbst in Gippsland, including the classic Bells Headland to Bird Rock coastal section, near Torquay and the Tertiary in the Geelong area. We believe that our records of occurrence for *Alataleberis* are as accurate as we can make them, a corollary of this being that the genus does not occur east of the Western Port Basin—at least in outcrop, since we have not viewed Gippsland Basin borehole material.

In assessing the stratigraphic usefulness of *Alataleberis* it is first necessary to determine the evolutionary sequence. In our opinion, the most plausible ancestor for the group is *A. robusta*. This taxon is facies transgressive and the earliest to appear since we have it from about 8 m below the *Notostraea* Greensand member at Browns Creek. This member is the equivalent of the Tortachilla Limestone at Maslin Bay and both units have been dated recently as P16 (Late Eocene) based on calcareous nannofossils and the common occurrence of *Hantkenina* (H.) *alabamensis primitiva* Cushman & Jarvis (Shafik 1981). With *A. robusta* as ancestor, several evolutionary trends are evident.

1. Only *A. robusta* has a well-defined subcentral tubercle, the trend is to a poorly-defined subcentral tubercle in the other species
2. There is a decrease in size from Eocene to Miocene, *A. robusta* being the largest and *A. miocenica* the smallest species.
3. Carapace breadth also decreases with time. Thus *A. robusta* is broader than *A. ornithopetrae*; and *A. johannae* is broader than *A. miocenica*.
4. The buttressed dorsal ridge of *A. robusta* gives way to the strongly spinose dorsal ridge of *A. ornithopetrae* and this in turn to the less-strongly spinose ridges of *A. johannae* and *A. miocenica*.
5. The buttressed ventral ridge is distinctly perforated in the more alate and older taxa (*A. robusta*, *A. ornithopetrae*) but either imperforate or nearly so in *A. johannae* and *A. miocenica*.

The complex of characters defined in the set of trends listed above makes species of *Alataleberis* easy to identify. Since each species has a relatively limited time range, at least in Victoria, this makes them all stratigraphically useful, although (as might be expected) the control is not as precise as it would be if based on planktonic foraminiferans or nannofossils. An advantage of the ostracode *Alataleberis* is that the species are relatively large (0.75–1.10 mm) and easily recognisable in washings or "floats". Further, none of the species are facies restricted since all have been recorded from a variety of nearshore marl and limestone facies. These range from grits to clays and well-oxygenated to poorly oxygenated sediments. The relevant palaeotemperatures likewise are variable, from about 14–23°C (Gill 1968).

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PARANESIDEA AND PAPILLATABAIRDIA (CRUSTACEA, OSTRACODA) FROM THE MIOCENE OF THE PORT PHILLIP AND WESTERN PORT BASINS, VICTORIA, AUSTRALIA

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ABSTRACT: Three new bairdiid ostracode species are described, *Paranesidea barwonensis*, *Paranesidea epineritica*, and "*Paranesidea*" *vadum* from the late Early to early Middle Miocene Batesford Limestone, Fyansford and Sherwood Formations, south-central Victoria. The generic allocation of the last named species under *Paranesidea* rather than *Triebelina* is discussed. Their lithostratigraphic distributions indicate a shallow water palaeoecology. In addition, the first fossil occurrence of a species of *Papillatabairdia* is noted.

During the study of the ostracode faunas from the late Early to early Middle Miocene formations within the Port Phillip and Western Port Basins (Figs 1, 2) the author found several new species belonging to the genus *Paranesidea* Maddocks, 1969. These, together with the restricted occurrence of species belonging to *Bairdopilata*, make up a small, conspicuous element within the *Neonesidea*-dominated bairdiid ostracode faunas abundant in the Batesford Limestone and shallower water facies of the Fyansford and Sherwood Formations.

Paranesidea barwonensis sp. nov., although common in the Batesford Limestone, occurs more abundantly in the conformable Fyansford Clay outcropping below the limit of *Lepidocyclina* in the Batesford Limestone Quarry (22 specimens). The Fyansford Clay below the upper limit of *Lepidocyclina* is transitional in lithology and depth of deposition between the very shallow water Batesford Limestone and other deeper, inner to mid-shelf (?) units of the Fyansford Clay, such as occurring above the upper limit of *Lepidocyclina* (Bowler 1963). *Paranesidea barwonensis* is significantly less abundant in these deeper water depositional units, but the presence of adults together with late and early stage instars suggests that it is also part of the biocenosis in the Fyansford Clay above the upper limit of *Lepidocyclina*. Two adult specimens were found within the outer shelf to epibathyal Balcombe Clay, the deepest water facies of the Fyansford Formation, at Manyung Rocks near Mornington, but because of a lack of juveniles they are here assumed to be part of the thanatocenosis. Specimens are also common in the Flinders Limestone, considered to be part of the Sherwood Formation, outcropping on the coast near Flinders, Victoria. Conformable with the Flinders Limestone is the broadly termed Sherwood Marl, this being the other lithostratigraphic component of the Sherwood Formation. Although the Sherwood Marl contains an abundant ostracod fauna, no specimens of *Paranesidea barwonensis* were recovered.

Paranesidea epineritica sp. nov. is rare in comparison to *Paranesidea barwonensis*. However, adults and mainly late stage instars were found in the Batesford

and Flinders Limestones (10 specimens) and only juveniles in both the shallow and deeper water depositional units of the Fyansford Clay. "*Paranesidea*" *vadum* sp. nov. is most abundant in the Batesford Limestone (14 specimens), but is also common within the transitional shallow water units of the Fyansford Clay outcropping below the upper limit of *Lepidocyclina* in the Batesford Limestone Quarry and is very rare in the deeper water units outcropping above the upper limit of *Lepidocyclina*. It is conspicuous in the Flinders Limestone, but rare in the Sherwood Marl. No early stage instars have been found although all the localities yield both adult and late stage instars excepting those of the Sherwood Marl where only single adult specimens have been found. The lack of early stage instars may be because this species is small, and also because specimens are generally found in the high energy shallow water facies. It is therefore inferred that early stage ecapaces once shed, and no longer stabilized by the biological activity and weight of the living animal, were easily transported and/or destroyed. However, van den Bold (1974) in noting the rarity of early *Triebelina* moults (some species closely resembling this new "*paranesidean*" form) suggested they were indistinguishable from the early moults of some non-ornate bairdiids. No specimens were found in the Balcombe Clay, this outer shelf to epibathyal facies representing a depth of deposition which was spatially far removed from the environments containing these essentially shallow water forms.

One single (juvenile?) right valve of a *Papillatabairdia* species was recovered from the Middle Miocene of the Sherwood Marl. This species closely resembles the Recent species described by Bentley (1981), *Papillatabairdia dentata* and previously referred to as *Bythocypris* sp. (Hartmann-Schroeder & Hartmann 1978).

The presence of species from these two genera within the Victorian late Early to early Middle Miocene is in accord with the tropical to subtropical climatic affinities of the ostracode assemblages described for this period of deposition (McKenzie 1974, Whitley & Downing 1983, McKenzie & Peypouquet 1984).

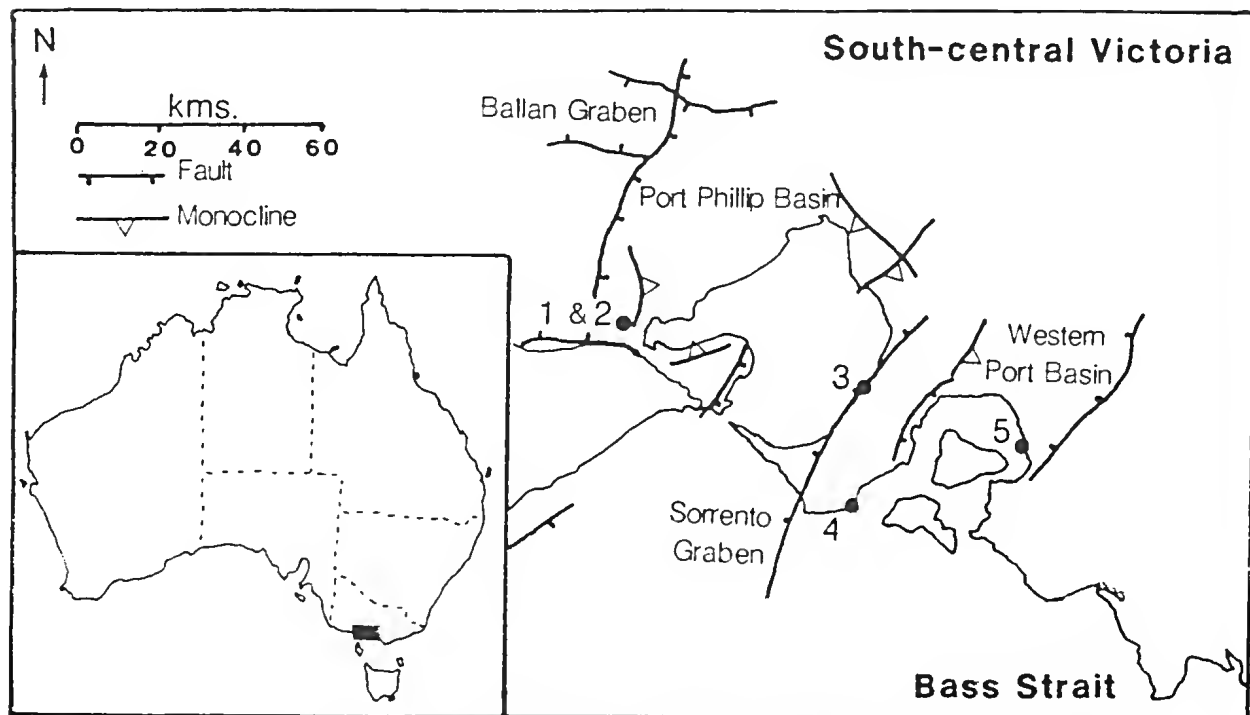


Fig. 1—Map showing sample localities. 1, 2, Batesford Limestone Quarry. 3, Manyung Rocks, Morn-
ington. 4, Flinders. 5, Victorian Geological Survey Borehole "Lang Lang 28".

The new species of "*Paranesidea*" *vadum* displays carapace characters that are taxonomically transitional between the two genera *Paranesidea* and *Triebelina*. Its generic allocation is therefore provisional. This problem is commonly encountered in bairdiid species as noted by van den Bold (1974), and highlights the difficulty in distinguishing generically forms which display carapace features that change gradually between genera and may not completely correlate with variations in the soft part anatomy of modern species of these genera.

The conventions RV=right valve, LV=left valve, L=length, H=height, W=width are used throughout. Type specimens are housed in the F. A. Singleton Museum of the Geology Department at the University of Melbourne under the registered numbers MUGDFS 4164-MUGDFS 4179. Outcrop samples were approximately 0.5 kg dry weight.

SYSTEMATIC PALAEOONTOLOGY

Family BAIRDIDAE Sars, 1888
Genus *Paranesidea* Maddocks, 1969
Paranesidea barwonensis sp. nov.
Figs 3 A-I, 4 A-B

ETYMOLOGY: The type locality is near the Barwon River, Fyansford, Victoria.

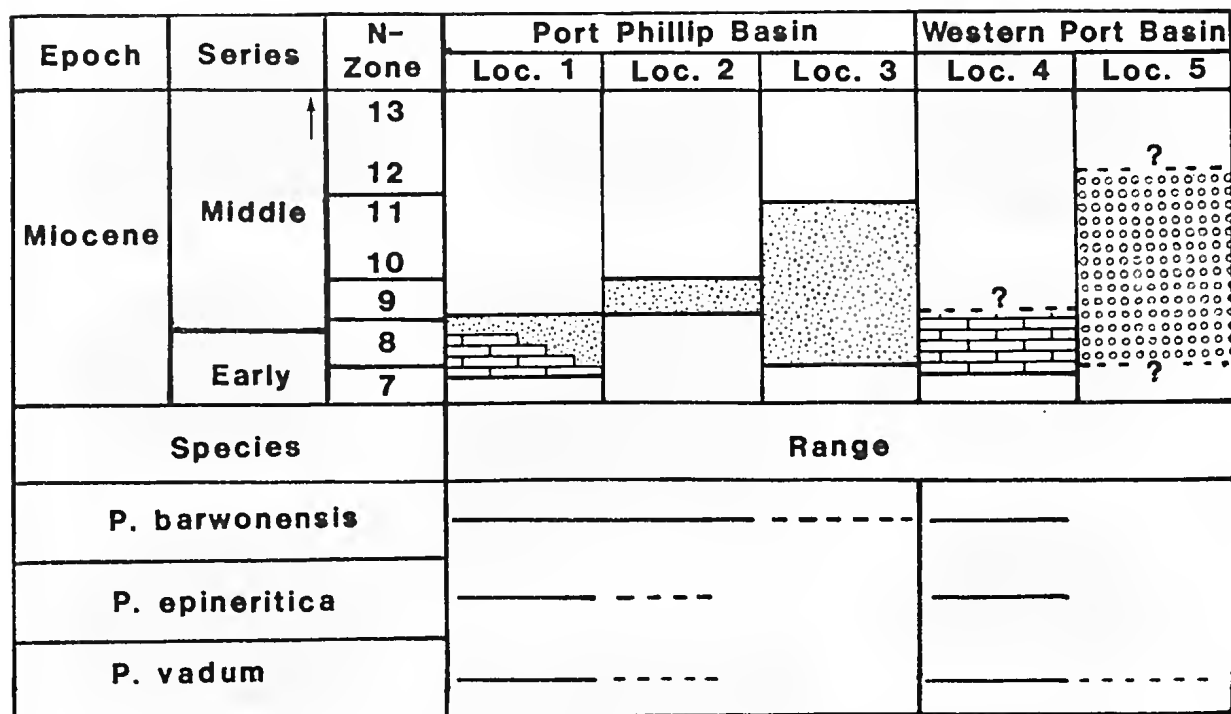
MATERIAL: Seventy, both adult and juvenile, specimens from the Batesford Limestone, Fyansford and Sherwood Formations, Victoria.

DIAGNOSIS: Characterised by its short carapace, weak caudal extension and spinose anterior and posterior

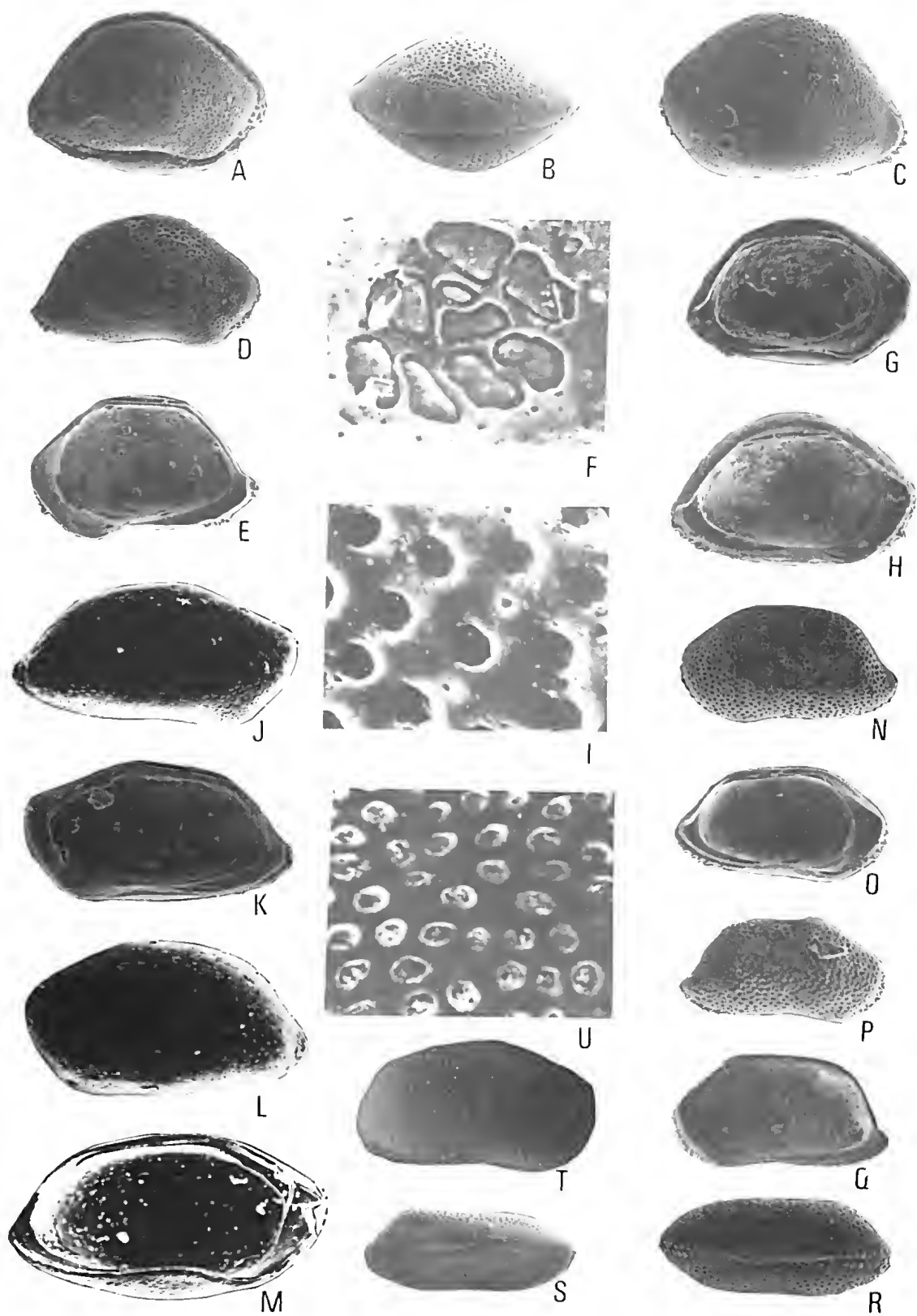
margins on both left and right valves.

DESCRIPTION: Carapace robust, coarsely punctate, inflated, rotund, and moderately small for family. LV larger than RV and overlapping it. LV with symmetrical rounded anterior, straight anterodorsal and convex anteroventral slope; extremity at mid-height. Posteriorly LV with convex posterodorsal slope and weakly developed caudal extension well below mid-height. Anteriorly RV with straight anterodorsal slope and straight to slightly convex anteroventral slope. Posteriorly RV with straight posterodorsal slope, short convex posteroventral slope and caudal extension below mid-height. Dorsal margin highly arched in LV, less so in RV. Maximum height at mid-length; maximum length just below mid-height; maximum width distinctly ventral. Normal pore canals simple without rims, large and numerous. Inner lamellae moderately broad, inner margin more rounded than outer margin; vestibulum narrow; marginal pore canals simple, straight and numerous. Selvage prominent and sinuous ventrally. Hinge lophodont in adults; adont in juveniles. Anterior and posterior margins denticulate in both valves. Adductor muscle scars comprising eight to nine, occasionally divided, subrounded to elongate scars in an overall subrounded pattern. Sexual dimorphism pronounced with males being more elongate and less inflated in the ventral region than females.

DIMENSIONS: Holotype, male, MUGDFS 4164, L=0.74 mm, H=0.47 mm, W=0.43 mm. Paratype, LV, female, MUGDFS 4165, L=0.76 mm, H=0.49 mm. Paratype, RV, male, MUGDFS 4166,



DESCRIPTION: Thick shelled carapace of moderate size, elongate; ventral region slightly inflated; finely punctate. LV larger than RV and overlapping it. LV with asymmetrically rounded anterior, straight to slightly concave anterodorsal slope and convex anteroventral slope; extremity above mid-height. Posteriorly LV with slightly concave posterodorsal slope, very short convex posteroventral slope and weakly developed caudal extension well below mid-height. RV with asymmetrically rounded anterior, but narrower than in LV with straight to slightly concave anterodorsal slope, convex anteroventral slope; extremity at mid-height. Posteriorly



RV with convex posterodorsal slope; short convex posteroventral slope and caudal extension below mid-height. Dorsal margin straight in RV, gently arched in LV. Ventral margin straight in LV, slightly indented in RV. Maximum length above mid-height in LV; approximately at mid-height in RV. Maximum height anterior of mid-length. Maximum width distinctly ventral. Normal pore canals simple without rims, large and numerous. Inner lamellae of moderate size, inner margin subparallel to outer margin; vestibulum distinct, larger in the anterior than in the posterior. Marginal pore canals simple, straight and numerous. Selvage prominent and straight to gently sinuous in ventral region. Overall marginal denticulation is quite variable, occurring on the posteroventral and anteroventral slopes of both valves. Spines on well preserved juvenile specimens are generally long, pointed and fragile while those on adults are short, broad, rounded and more robust. Hinge lophodont in adults; adont in juveniles. Adductor muscle scars below mid-height and slightly anterior of mid-length comprising eight to nine subrounded to wedge-shape scars in a subrounded aggregate. Sexual dimorphism slight with males being more elongate than females which have a more rounded dorsal margin.

DIMENSIONS: Holotype, RV, female, MUGDFS 4170, L=0.85 mm, H=0.35 mm. Paratype, RV, juvenile?, MUGDFS 4171, L=0.80 mm, H=0.33 mm. Paratype, LV, juvenile?, MUGDFS 4172, L=0.80 mm, H=0.34 mm. Paratype, LV, female, MUGDFS 4173, L=0.85 mm, H=0.37 mm.

TYPE LOCALITY: Batesford Limestone in Batesford Limestone Quarry one metre above base of Quarry, south-west face, near Fyansford, Victoria, 38°06'S, 144°17'E.

REMARKS: The marginal spinosity in this taxon is variable and sometimes absent. Absence is probably an effect of taphonomy, but variation in the degree of spinosity possibly correlates with physiological and environmental factors.

Intraspecific variation of marginal denticulation in the genus has been previously noted by van den Bold

(1974). *P. epineritica* is unlike *P. barwonensis* which is less elongate and more coarsely punctate, and differs from the superficially similar figured but undescribed *Bairdia* sp. 179 (Hartmann 1981) in outline and marginal ornament. This new species is also present in the marly facies of the Muddy Creek Miocene, Hamilton, Victoria (personal communication J. V. Neil 26-7-85). Two juvenile? specimens from the Fyansford Clay (from type locality of *P. barwonensis*) are included as paratypes as these demonstrate the punctate ornament not shown by the abraded adults from limestone facies.

GEOLOGICAL AGE: Batesfordian to Balcombian (N8-9), late Early to early Middle Miocene.

"*Paranesidea*" *vadum* sp. nov.

Figs 3 N-S, 4 E-F, H-M

ETYMOLOGY: *Vadum* (Latin) — shallow water, a reference to the presumed shallow water habitat of the species.

MATERIAL: Twenty-eight adults and late stage juveniles from the Batesford Limestone, Fyansford and Sherwood Formations.

DIAGNOSIS: Characterised by a triebelinan shape (subquadrate) but without distinct ridges or swellings on lateral surface.

DESCRIPTION: Carapace small, very robust, coarsely punctate, almost equivalved and subquadrate in lateral outline. LV slightly larger than RV. LV with acutely rounded anterior, straight anterodorsal slope and convex anteroventral slope, extremity at mid-height. Posteriorly LV with posterodorsal slope concave, posteroventral slope convex and caudal extension below mid-height. Dorsal margin straight, ventral margin concave. RV similar in outline to LV excepting it is more elongate, more caudate, and has a pronounced indentation of the ventral margin. Maximum length slightly below mid-height; maximum height at mid-length, maximum width below mid-height in ventral region and approximately equal to the width of the carapace in the slightly swollen posterodorsal region of the LV (see below).

Fig. 3—A, *Paranesidea barwonensis* sp. nov., male, lateral view of entire carapace, $\times 54$, MUGDFS 4164 (Holotype). B, *Paranesidea barwonensis* sp. nov., male, dorsal view of entire carapace, $\times 51$, MUGDFS 4164 (Holotype). C, *Paranesidea barwonensis* sp. nov., female, external LV, $\times 50$, MUGDFS 4165 (Paratype). D, *Paranesidea barwonensis* sp. nov., male, external RV, $\times 54$, MUGDFS 4166 (Paratype). E, *Paranesidea barwonensis* sp. nov., female, internal RV, $\times 51$, MUGDFS 4167 (Paratype). F, *Paranesidea barwonensis* sp. nov., male, muscle scar RV, $\times 210$, MUGDFS 4166 (Paratype). G, *Paranesidea barwonensis* sp. nov., female, internal LV, $\times 48$, MUGDFS 4168 (Paratype). H, *Paranesidea barwonensis* sp. nov., male, internal LV, $\times 52$, MUGDFS 4169 (Paratype). I, *Paranesidea barwonensis* sp. nov., female, surface ornament and normal pore canals LV, $\times 450$, MUGDFS 4165 (Paratype). J, *Paranesidea epineritica* sp. nov., external RV juvenile?, $\times 53$, MUGDFS 4171 (Paratype). K, *Paranesidea epineritica* sp. nov., female, internal RV, $\times 49$, MUGDFS 4170 (Holotype). L, *Paranesidea epineritica* sp. nov., external LV juvenile?, $\times 55$, MUGDFS 4172 (Paratype). M, *Paranesidea epineritica* sp. nov., female, internal LV, $\times 55$, MUGDFS 4173 (Paratype). N, "*Paranesidea*" *vadum* sp. nov., female, external LV, $\times 49$, MUGDFS 4175 (Paratype). O, "*Paranesidea*" *vadum* sp. nov., male, internal LV, $\times 50$, MUGDFS 4176 (Paratype). P, "*Paranesidea*" *vadum* sp. nov., male, external RV, $\times 48$, MUGDFS 4177 (Paratype). Q, "*Paranesidea*" *vadum* sp. nov., female, internal RV, $\times 48$, MUGDFS 4178 (Paratype). R, "*Paranesidea*" *vadum* sp. nov., male, ventral view of entire carapace, $\times 56$, MUGDFS 4174 (Holotype). S, "*Paranesidea*" *vadum* sp. nov., male, dorsal view of entire carapace, $\times 50$, MUGDFS 4174 (Holotype). T, *Papillatabairdia* sp. cf. *dentata* external RV, $\times 70$, MUGDFS 4179. U, *Papillatabairdia* sp. cf. *dentata*, surface ornament RV, $\times 700$, MUGDFS 4179.

The ventral region of both valves is longitudinally but indistinctly swollen with slight increases in degree posteroventrally and anteroventrally, the former being greater than the latter. No distinct ventrolateral carina is developed. Slight posterodorsal swelling present; greater in LV than RV. Lateral surface region anterior of posterodorsal swelling is very greatly depressed in some specimens from the mid-dorsum down to mid-length of ventrolateral swelling. This ornamental feature (depression) is only visible in dorsal and ventral perspectives of adult males, adult females being also inflated in the mid-carapace region, hence obscuring the very subtle undulations present in the male. Inner lamellae large in relation to overall size; inner margin subparallel to outer margin; vestibule narrow. Marginal pore canals simple without rims, large and numerous. Selvage prominent and sinuous ventrally. Hinge lophodont in adults; adont in juveniles. Stout spines on the posteroventral and anteroventral margins of both valves. Adductor muscle scar complex consisting of eight to nine occasionally divided, subrounded to elongate scars in a subcircular aggregate. Presumed sexual dimorphism slight but detectable, in that the females tend to be higher, have a steeper posterodorsal slope and are slightly more swollen in the mid-carapace region than the males, which are relatively more elongate.

DIMENSIONS: Holotype, male, MUGDFS 4174, L=0.65 mm, H=0.35 mm, W=0.27 mm. Paratype, LV, female, MUGDFS 4175, L=0.66 mm, H=0.36 mm. Paratype, LV, male, MUGDFS 4176, L=0.65 mm, H=0.35 mm. Paratype, RV, male, MUGDFS 4177, L=0.64 mm, H=0.29 mm. Paratype, RV, female, MUGDFS 4178, L=0.66 mm, H=0.31 mm.

TYPE LOCALITY: Fyansford Clay in Batesford Limestone Quarry, near the base of the formation at this location (below upper limit of *Lepidocyclina*), one metre vertically above the contact with the Batesford Limestone, south-west face, near Fyansford, Victoria, 38°06'S, 144°17'E.

REMARKS: This species differs from *Paranesidea* sp. (van den Bold 1974) which has a gently arched dorsal margin and is less caudate. It is unlike *Bairdia* sp. (Allison & Holden 1971) which is more elongate, less caudate and has an evenly rounded lateral surface. *Paranesidea parva* Hartmann-Schroeder and Hartmann, 1978 differs in having among other distinctive features, a higher posterior extremity and a more rotund shape. In general, this new taxon contrasts with species belonging to the genus *Triebelina* originally described by van den Bold (1946) because these have a stronger surface ornament often with a distinct ventrolateral carina. However, the subtly developed undulations and swellings on the male carapace of the new species perhaps tend towards the surface ornament of some *Triebelina* species such as *Triebelina boldi* Keij. Significantly one cluster of *Triebelina* species (Keij 1974) having relatively long carapaces and weakly or only partially developed ventrolateral carinac, and including *T. boldi* as well as *T. reticulopunctata*, *T. howei*, *T. crumena* and *T. bradyi*,

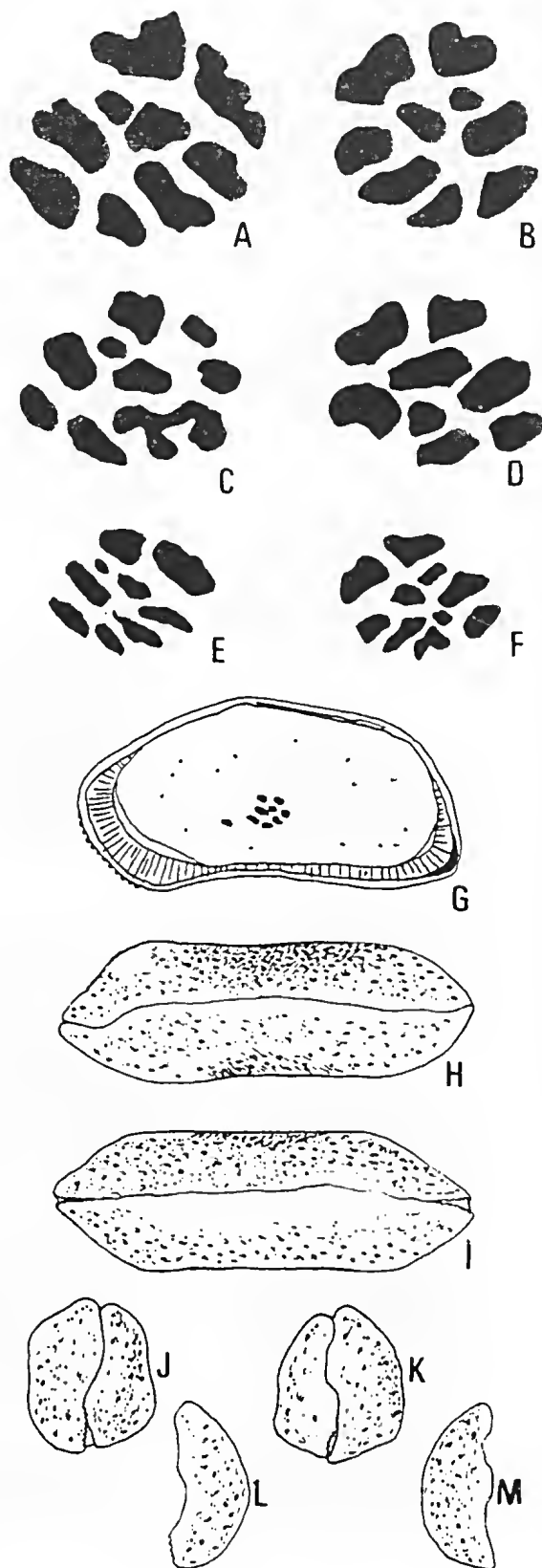


Fig. 4—A, *Paranesidea barwonensis* sp. nov., RV muscle scar, $\times 200$, MUGDFS 4167 (Paratype). B, *Paranesidea barwonensis* sp. nov., LV muscle scar, $\times 200$, MUGDFS 4169 (Paratype). C, *Paranesidea epineritica* sp. nov., RV muscle scar, $\times 205$, MUGDFS 4170 (Holotype). D, *Paranesidea epineritica* sp. nov., LV muscle scar, $\times 205$, MUGDFS 4173 (Paratype). E, "*Paranesidea*" *vadum* sp. nov., RV muscle scar, $\times 195$, MUGDFS 4178 (Paratype). F, "*Paranesidea*" *vadum* sp. nov., LV muscle scar, $\times 195$, MUGDFS 4176 (Paratype). G, *Papillatabairdia* sp. cf., *dentata*, internal RV, $\times 98$, MUGDFS 4179. H, "*Paranesidea*" *vadum* sp. nov., dorsal, male, $\times 86$, MUGDFS 4174 (Holotype). I, "*Paranesidea*" *vadum* sp. nov., ventral, male, $\times 86$, MUGDFS 4174 (Holotype). J, "*Paranesidea*" *vadum* sp. nov., posterior, male, $\times 65$, MUGDFS 4174 (Holotype). K, "*Paranesidea*" *vadum* sp. nov., anterior, male, $\times 65$, MUGDFS 4174 (Holotype). L, "*Paranesidea*" *vadum* sp. nov., posterior, female, RV, $\times 67$, MUGDFS 4178 (Paratype). M, "*Paranesidea*" *vadum* sp. nov., anterior, female, RV, $\times 67$, MUGDFS 4178 (Paratype).

were considered by Keij to be the closest morphological group to *Paranesidea*. Furthermore, the very small robust carapace of this new species together with its sub-quadrate outline is more akin to taxa belonging to *Triebelina* than to *Paranesidea*, especially in the context of Maddocks' (1969) definitions. Nevertheless, the viewpoint of van den Bold (1974), in which he questioned the significance of, and therefore altered the emphasis on, diagnostic triebelina features, is accepted in this paper. Van den Bold concluded that only those forms with distinct ridges and swellings should be allocated to *Triebelina*. This new species is therefore placed under *Paranesidea*, although morphologically transitional towards *Triebelina*. The recorded biostratigraphic distribution of strongly ornamented Indo-Pacific bairdiids (i.e. *Triebelina sensu* van den Bold and Keij) begins in the Late Miocene indicated by *T. sertata* from the Philippines and *T. bradyi* from the Fijian Islands (Keij 1973). Although earlier occurrences have been documented outside this region (Keij 1974), it is not until post-Middle Miocene times that distinct *Triebelina* forms become evident within the Indo-Pacific region. The placement of this new Middle Miocene species under *Paranesidea* therefore accords with the stratigraphic framework. The general trend towards increasing distribution upsequence of heavily ornate bairdiids such as *Triebelina* in the region is also reflected in the records of *Havanardia* and *Pterobairdia* (Keij 1973, 1976, McKenzie & Keij 1977).

This new species is also present in the marly facies of the Muddy Creek Miocene, Hamilton, Victoria (personal communication J. V. Neil 26-7-85).

GEOLOGICAL AGE: Batesfordian to Baleombian (N8-9), late Early to early Middle Miocene.

Genus *Papillatabairdia* Bentley, 1981

Papillatabairdia sp. cf. *dentata* Bentley, 1981

Figs 3 T-U, 4 G.

MATERIAL: One RV from the Middle Miocene Sherwood Formation (marly facies) in the Geological Survey of Victoria borehole "Lang Lang" 28 between the intervals 72 and 74 metres from the surface.

DIMENSIONS: RV, juvenile? MUGDFS 4179, L=0.53 mm, H=0.29 mm.

REMARKS: Small reasonably thick shelled papillate form with a truncated posterior. Differs from *Papillatabairdia dentata* Bentley, 1981 in being smaller, more elongate, having a less rounded posterior, higher anterior extremi-

ty and greater cardinal angle between the dorsal and anterodorsal margins. The significance of these differences may be no more than an indication of juvenility.

GEOLOGICAL AGE: Middle Miocene.

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I also acknowledge financial assistance from the Commonwealth Postgraduate Research Award Scheme; and the Department of Geology at the University of Melbourne for the use of facilities.

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SHORT COMMUNICATION

MEGASTEGER SEPTENTRIONALIS (ETHERIDGE, 1907), A PERMIAN BRACHIOPOD FROM THE NORTHERN TERRITORY REDESCRIBED

Robert Etheridge Junior's (1907) *Aulosteges baracoodensis* var. *septentrionalis* was not discussed by Coleman (1957) in his extensive study of Western Australian aulostegid brachiopods. Etheridge's (1907) original publication is rather obscure and it was not realized until recently that most of the type material from his Port Keats collection is housed in the South Australian Museum. Hosking (1933) had earlier been unable to locate most of the specimens. The purpose of the present note is to redescribe and reillustrate most of Etheridge's (1907) specimens, elevate the variety *septentrionalis* to full specific rank and assign the species to *Megasteges* Waterhouse (1975).

STRATIGRAPHY, LOCALITIES AND AGE

The onshore Permian stratigraphy of the Port Keats District, Northern Territory, has been elucidated by Thomas (1957) who reviewed earlier work and discussed the faunal zones present in the sequence. Dickins *et al.* (1972) reviewed earlier work and recorded an additional faunal horizon. The type material of *Megasteges septentrionalis*, from Cape Dombey, comes from the Upper Marine Beds of the Port Keats Group and is associated with fossil Assemblage D, as discussed by Thomas (1957, 1958). Assemblage D is Early Tatarian or Chhidruan in age (i.e. immediately younger than Kazanian) and is readily correlated with the faunas of the Hardman Formation of the Canning Basin and the Chhidru Formation of the Salt Range, Pakistan (Thomas, 1958). A specimen from Cape Ford assigned to *Strophalosia?* sp. by Etheridge (1907) is reillustrated herein and is interpreted as an incomplete dorsal valve of *Megasteges septentrionalis*. The Permian strata at Cape Ford appear to be the same age as those at Cape Dombey (Dickins *et al.* 1972).

SYSTEMATIC PALAEOONTOLOGY

Superfamily AULOSTEGACEA Muir-Wood & Cooper 1960

Family AULOSTEGIDAE Muir-Wood & Cooper 1960

Genus *Megasteges* Waterhouse 1975

TYPE SPECIES: *Megasteges nepalensis* Waterhouse 1975.

DIAGNOSIS: The diagnosis provided by Waterhouse (1975, p. 6) is accepted except for the modification that the huge ventral diductor scars do not always fuse anteriorly of the ventral adductor scars.

DISCUSSION: *Megasteges* has been discussed and illustrated by Waterhouse (1978) and has since been recognised in the Permian faunas of Queensland (Waterhouse *et al.* 1983).

Megasteges septentrionalis (Etheridge 1907)

Fig. 1A-F

1907 *Aulosteges baracoodensis* var. *septentrionalis* Etheridge p. 6, pl. 1, figs. 1-5.

1907 *Strophalosia?* sp. Etheridge, p. 6, pl. 1, fig. 6.

1933 *Aulosteges baracoodensis* var. *septentrionalis* Etheridge; Hosking, p. 35.

1957 *Aulosteges ingens* Hosking; Coleman (*partim.*), p. 43, pl. 3, figs. 5, 7, 9, 10 (*non cet.*).

1957 *Aulosteges reclinis* Coleman (*partim.*), p. 38, pl. 6, fig. 1 (*non cet.*).

cf. 1957 *Aulosteges fairbridgei* Coleman (*partim.*), p. 40, figs. 11-12 (*non cet.*).

LECTOTYPE: SM P2135 an internal mould of a conjoined shell (Fig. 1A-B), chosen herein.

MATERIAL: Etheridge's re-examined type material consists of: SM P2135, the lectotype; SM P2136, a natural cast of a decorated shell; SM P2137, a natural cast of a ventral valve and SM P2125, a natural cast of an incomplete dorsal valve interior (figured by Etheridge as *Strophalosia?* sp.).

MEASUREMENTS (in mm): See Table 1.

DIAGNOSIS: Large *Megasteges* with variable outline. Sulcus gentle. Shell outline rounded in maturity.

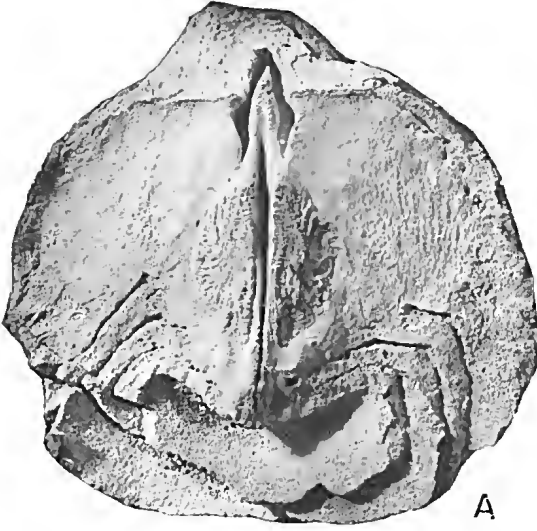
DESCRIPTION: Shell large, variable in outline although rounded in maturity. Ventral umbo distinct and may be twisted over high, variably inclined, ventral interarea. Interarea gently concave and bisected by poorly known, high, narrow, triangular convex pseudodeltidium. Dorsal valve gently convex posteriorly, concave, around anterior visceral disc and curves abruptly into poorly known, geniculate trail. Dorsal valve appears to lack interarea. Ventral sulcus, which arises some 2 cm in front of umbonal tip, shallow, wide and gently rounded in cross-section. Ventral spines which cover the entire valve, arranged in illdefined quincunx. Spine base elongate (up to 8 mm) and spines were probably recumbent. Spine bases up to 1.1 mm wide.

Ventral adductor platform gently raised, relatively narrow, scored with ridges and grooves and subdivided by thin median groove. Diductor impressions large, laterally and anteriorly placed but not fused in front of adductors; marked by ridges and grooves radiating forward.

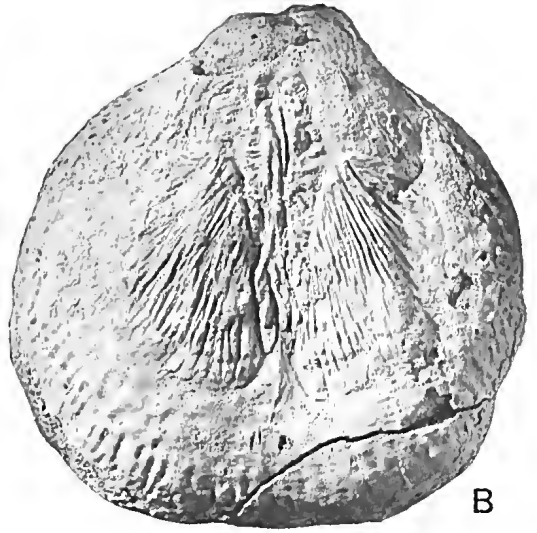
Cardinal process large with two anterior lateral supports. Median septum arises in between lateral supports and persists anteriorly for at least seven eighths of valve length. Dorsal ad-

TABLE 1
MEASUREMENTS OF *Megasteges septentrionalis*. * = lectotype; e = estimate; + = incomplete specimen

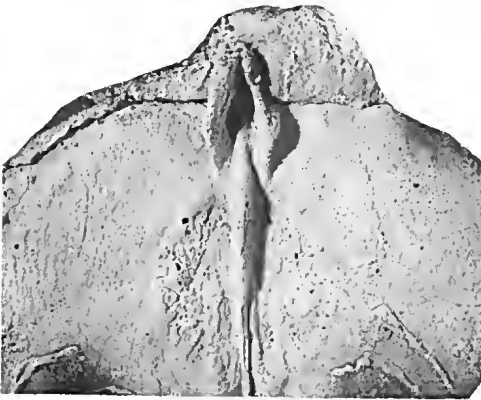
Specimen Number	Hinge Width	Maximum Width	Ventral Length	Dorsal Length	Thickness	Length Dorsal Septum
SM P2135*	35e	67	69	57	24	43 +
SM P2136	28	52	59	45	—	38
SM P2137	—	47	63	—	—	—
SM P2125	—	50	—	41 +	—	34 +



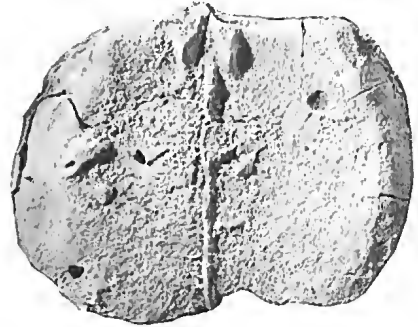
A



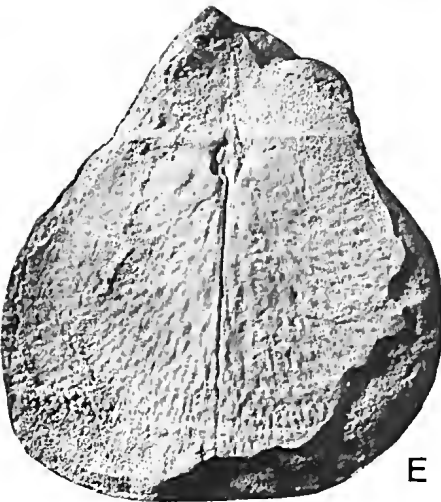
B



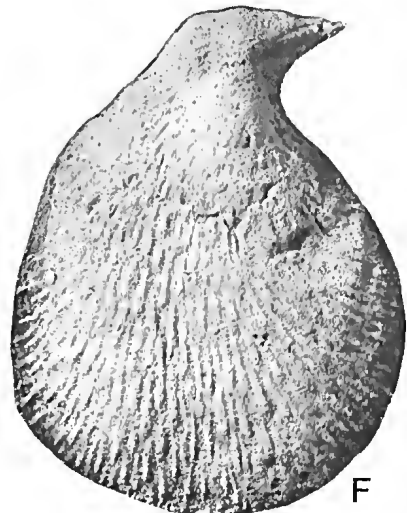
C



D



E



F

Fig. 1—A-F, *Megasteges septentrionalis* (Etheridge): A-F, from Upper Marine Beds, Port Keats Group, Bonaparte Gulf Basin. A-C, SM P2135 lectotype, internal mould of shell in dorsal and ventral views and enlargement of latex cast of dorsal interior, $\times 1$, $\times 1$ and $\times 3$. D, SM P2125, natural cast of dorsal valve interior, $\times 1$ (figured by Etheridge, 1907, as *Strophalosia?* sp.). E, SM P2136, natural cast of decorticated shell in dorsal view, $\times 1$. F, SM P2137, natural cast of ventral valve in ventral view, $\times 1$.

ductor scars strongly dendritic, poorly differentiated. Brachial ridges unknown.

Discussion: *Megasteges septentrionalis* is a variable species and large collections are required in order to elucidate the ontogeny of the species. Figured specimens of aulostegids from the Port Keats Area attributed by Coleman (1957) to *Aulosteges ingens* appear to belong to Etheridge's species on the basis of dorsal interior features. Species described by Coleman (1957) such as *Aulosteges fairbridgei* and *Aulosteges reclinis*, both from the Hardman Formation of the Canning Basin, share much in common with *M. septentrionalis*, and may be junior subjective synonyms. However, only the analysis of large collections from both the Hardman Formation and the Upper Marine Beds, Port Keats Group will clarify any such synonymy, a task beyond the purpose of this note.

Megasteges nepalensis Waterhouse (1975, 1978) is distinguished from *M. septentrionalis* by means of its more pronounced sulcus and ventral diductor scars that fuse anteriorly of the ventral adductor scars. *M. randsi* (Hill, 1950 pl. 6 figs. 1-2; see also Waterhouse *et al.*, 1983) recalls elongate examples of *septentrionalis* but is known only from ventral valves.

The ventral valve of *M. septentrionalis* stated by Hosking (1933) to be housed in the Australian Museum cannot now be traced (Mr. R. K. Jones, pers. comm. 30-05-85).

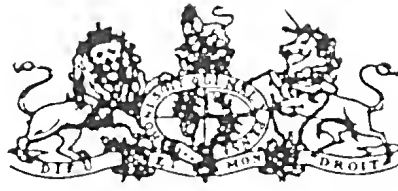
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I thank Dr. B. J. Cooper, Geological Survey of South Australia for assisting in tracing Etheridge's specimens and Dr. N. Pledge, South Australian Museum for arranging the loan of material. Dr. A. Ritchie and Mr. R. K. Jones attempted to locate the missing ventral valve in the Australian Museum.

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VERTEBRATE FAUNA OF THE SILVERBAND FORMATION, GRAMPIANS, WESTERN VICTORIA

By SUSAN TURNER

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ABSTRACT: Scales from the Grampians Group of western Victoria, previously reported as shark denticles, are predominantly those of a new species of turiniiform thelodont, *Turinia fuscina*, similar to those of the Late Silurian-Early Devonian *Turinia pagei* (Powrie), and possibly those of an ischnacanthiid acanthodian, possibly *Gomphonchus*. Tooth whorls in the Silverband Formation probably also belonged to *Gomphonchus*. Fin spines, identified hitherto as the elasmobranch *Physonemus*, are possibly climatiid acanthodian remains; they resemble those of *Sinacanthus* from the Siluro-Devonian of China. An alternative interpretation of some of the scales and spines as those of an elasmobranch similar to *Antarctilamna* is considered. The age of the Silverband Formation is reassessed in the light of the new identifications of the vertebrate remains, and the environment of the fauna is discussed. Based on the presence of turiniiform scales an age range for the Silverband Formation from Gedinnian into early Frasnian is possible.

In 1917 Ferguson recorded the first fossils in the Grampians Group of western Victoria. He had found invertebrates and vertebrate macrofossils from one locality on the Stairway track to Mount Rosea in Unit 3 of the Silverband Formation (Ferguson 1917, Spencer-Jones 1965). Chapman (1917) identified the fauna as including "worm burrows", *Lingula squamiformis* Phillips var. *borungensis*, which "formed sheets on the bedding planes", and elasmobranch fin spines *Physonemus attenuatus* Davis and *Physonemus micracanthus* sp. nov.

As Spencer-Jones put it, Chapman "confidently gave a Lower Carboniferous age to these fossils" on the basis of the fin spines and brachiopods (Spencer-Jones 1965). The age determination and status of Chapman's identification of the *Lingula* species were queried, and from them only an inconclusive Devonian or Carboniferous age was extracted (Talent & Spencer-Jones 1963). Talent and Spencer-Jones (1963) discovered and described further material from six localities in Unit 3 and showed that Chapman's assessment of the age and content of the Silverband fauna was erroneous. The "worm burrows" were probably linguloid; the species of *Lingula* was unlike that of the Upper Devonian/Early Carboniferous; the spines were not those of *Physonemus* (Baird 1957, Talent & Spencer-Jones 1963). New finds of ostracodes and fish scales and teeth were described. Talent and Spencer-Jones still considered the vertebrate remains to be those of sharks and retained the use of '*Physonemus*' for the spines. They attempted to relate the scales they found to shark dermal denticles then known from the Palaeozoic but were not able to resolve them beyond Order Cladoselachii or Selachii. At that time shark remains were thought to be unknown in sediments older than Middle Devonian. Thus Talent and Spencer-Jones set a lower limit to the age of the Silverband Formation of Middle Devonian while retaining the suggested possible age of Upper Devonian through Lower Carboniferous (Spencer-Jones 1965, 1976).

Spencer-Jones (1976) summarized the fauna as *Lingula borungensis* (Chapman), two smooth ostracodes, spines of '*Physonemus*' *micracanthus* (Chapman), elasmobranch dermal denticles and teeth of apparent

elasmobranch affinities. The *Lingula* band occurs within thin purplish siltstones cropping out beneath the cliffs of the Wonderland Range whereas the fish and ostracodes occur together in Unit 3 beds south of Middleton Peak in the Serra Range and southwards to Mirranatwa Gap; ostracodes also occur in beds beneath Briggs Bluff and in the Asses Ears anteline (Spencer-Jones 1976, fig. 4.10).

THE SILVERBAND FISH FAUNA

The fish remains in the samples of Unit 3 of the Silverband Formation are preserved in a thin band of orange to pink quartzite. The scales and spines are chalky white and very friable and can only be prepared by mechanical means. The quartz grains are poorly cemented allowing the smaller scales to be removed from the matrix with a fine needle. Because of the nature of the material it has not been possible to see the larger specimens of scales, 'teeth', and spines in the round, and thin sectioning to examine histological structure has not been attempted. For these reasons it is not easy to decide on the identity of the remains, other than the small scales, with any degree of certainty. Therefore I am presenting alternative explanations for some of the remains. There are then two possible conclusions about the age of the Silverband Formation within the overall time span governed by the presence of turiniid remains. Only the discovery of better-preserved material will help to resolve the dichotomy.

Most of the smaller (<1.00 mm) scales from the Silverband Formation are not from elasmobranchs but belonged to the jawless fish called thelodonts. The fin spines, a few of the larger scales, and the tooth whorls can also be interpreted as non-elasmobranch remains. In 1981 I investigated the scales in the type material, having considered that the scales portrayed by Talent and Spencer-Jones were unlike those of any Devonian shark but were more akin to thelodont scales (Turner 1982a). Agnathan thelodonts were common elements of littoral and fluvial environments from the Early Silurian through to Late Devonian and were widespread especially in the Early into Middle Devonian (e.g. Turner 1973,

Tarling & Turner 1982). Shark scales are now known in the Late Silurian and Early Devonian but none is exactly like the simple placoid scales of thelodonts (Karatajute-Talimaa 1973, 1977, Vieth 1980). The Silverband scales belong to the genus *Turinia*, a thelodontid which is common in shallow-water Devonian sediments. The scales are referred here to a new species which is considered to be close to *T. pagei* (Powrie 1870) of the upper Pridoli and Lower Devonian of Europe and parts of North America, although in some features they resemble other Australian turiniid species.

A few scales observed in the Silverband Formation samples appear to be those of an acanthodian like *Poracanthodes* of Brotzen (1934); these scales are considered to be special scales of an ischnacanthid named *Gomphonchius* by Gross (1971a; Denison 1979). Alternatively, these larger scales might be those of a shark akin to *Antarctilamna* Young 1982.

The tooth whorls figured by Talent and Spencer-Jones (1963, pl. 11, figs 2, 3, 8) are also interpreted as those of an acanthodian. Many Early Devonian ischnacanthids possessed such tooth whorls, and even some climatiids such as *Nostolepis* are thought to have done so (Gross 1971a, Denison 1979). Other early bony fishes, such as onychodontid crossopterygians, also possessed tooth whorls, but in the absence of the typical conical teeth their presence is ruled out.

The fin spines are seen preserved in lateral view or in cross-section (Talent & Spencer-Jones fig. 3, pl. 11, figs 4-8). They are not like those of any Palaeozoic shark and are quite unlike those of *Physonemus* (St John & Worthen 1875, Baird 1957). One of the spines figured by Talent and Spencer-Jones (1963, pl. 11, fig. 5) is long and slender and might be that of an ischnacanthid (see Denison 1979). The other spines are relatively broad and arcuate, with a number of straight or slightly nodose dentine ribs along the exposed shaft, and have no obvious inserted portion. The illustrations given by Chapman (1917, pl. V, figs 1-3) seem to exaggerate the nodose ornament of the dentine ribs. The fin spines are similar to those of climatiids, and some referred to '*Orchilus*' (Denison 1979). Fin spines similar to these have been recorded by Young (1985) from the Amadeus Basin. However, the spines seem most like those called *Sinacanthus* P'an 1957, known from the Silurian and Early Devonian of China (Li 1980, Liu 1983). An alternative explanation, again based on overall shape and the poorly-preserved histological structure, is that the spines do belong to a shark akin to *Antarctilamna*.

ENVIRONMENT OF THE SILVERBAND FORMATION

Several early workers noted the similarity of the Silverband Formation and other sediments of the Grampians Group to the Old Red Sandstone of Britain (Chapman 1917, footnote 2). Talent and Spencer-Jones (1963) considered that Silverband Formation fauna was a "restricted fauna with marine affinities", with an overall assessment that the sediments of the Grampians Group are predominantly freshwater. Unit 3 consists of 55 m of

purplish-red, yellow or grey micaceous siltstone with some mudstone, containing 'clay galls', mudcracks and animal burrows. The combination of trace fossils, lingulids, ostracodes and fish is a common one in the Palaeozoic (Denison 1956). Allen (1985) described this combination as typical of the lower part of the Downton beds of the Welsh Borderland. Talent and Spencer-Jones regarded the Silverband fauna as a shallow-marine fauna, although Spencer-Jones (1965, p. 69) pointed out that the "appearance of mud cracks and clay galls is evidence that at some stage the sediments were above water level for sufficient time to allow desiccation" and implied tidal action was involved. The fish remains are scattered in small patches among the quartz grains of the sandstone band which probably forms the base of a purplish-red siltstone. The grains are subrounded and not strongly cemented. The thelodont scales are small by comparison with those of most other turiniid species. This decline in scale size has been observed elsewhere in sediments thought to be of hyposaline origin, as in the dolomitic limestones of Arctic Canada for instance (Turner pers. obs.).

According to Spencer-Jones (1976), the Grampians Group red beds are thickest in the Silverband Formation which he interpreted as possibly implying a period of slower sedimentation in a humid or semi-arid climate. The *Lingula* shells are disarticulated and mostly broken. Fragments of shells with pieces of fish spine are often associated with sediment in mudcracks. Chapman (1917) noted that the *Lingula* shells were often "crowded together in veritable sheets, having evidently drifted into small pools by tidal action". Spencer-Jones (1976) regarded these facts, associated with the mudcracks and clay galls, as indicating periodic desiccation and tidal action which would also concur with an estuarine or deltaic environment.

These facts gleaned from the sediments and the impoverishment of the fauna would seem to indicate that Unit 3 of the Silverband Formation was not formed in a typical marine environment but probably reflect hyposaline or brackish conditions, formed within an estuarine or intertidal environment (cf. Allen 1985). Plant remains of undoubted freshwater or terrestrial origin are present in the Grampians Group but occur some 3000 m above the Silverband Formation (Spencer-Jones 1965).

The association of thelodonts, climatiid and ischnacanthiid acanthodians, lingulids and ostracodes is not unusual in the Late Silurian and Early Devonian of the northern hemisphere (e.g. Denison 1956, Turner 1973, Märss & Einasto 1978). Märss and Einasto (1978) have assessed the environmental significance of the association and dominance of various elements in the very complete Early to Late Silurian sequence in Saaremaa. They regarded a combination of dominant thelodont scales with few acanthodian scales typical of near-shore conditions. Thus, whatever the actual sedimentary provenance of the Silverband Formation, it is reasonable to assume that the fish whose remains are found in Unit 3 were living in a shallow water, nearshore environment. After death their remains were swept into



Fig. 1—Location of major finds of thelodontids in Australia. Places marked—AS, Alice Springs; B, Brisbane; C, Canberra; M, Melbourne; P, Perth; S, Sydney. Brick motif for limestones; dots for sandstone/siltstones.

shallows possibly on the floodplain of the nearby continental shoreline.

Most of the thelodont scales found thus far in Australia come from nearshore or shallow water sediments (Fig. 1). The picture emerging from the study of Devonian thelodonts in Australia is one of turiniids, and possibly nikoliiviids, living mostly as isolated populations in different parts of the continent. *Turinia australiensis* Gross (1971b) was fairly widespread in Early Devonian times (Turner *et al.* 1981, Turner 1982b) but other turiniid species were already separate from these, as in the Grampians and also in northern Queensland (Turner pers. obs.). By late Early Devonian and Middle Devonian times other turiniid species are present in the Georgina (Turner *et al.* 1981), Amadeus, and Arckaringa Basins (Young pers. comm., Long pers. comm., Turner pers. obs.) and in the Hatchery Creek (Young &

Gorter 1981) and Broken River areas (Turner 1982c). By early Frasnian times only one thelodont population is known—in the Carnarvon Basin (Turner & Dring 1981). The separation of basins in the eastern part of Australia during the various Devonian orogenic events, discussed, for instance, by Cas (1983), probably created the right framework for turiniiform speciation.

AGE OF SILVERBAND FORMATION

On the purely sedimentary clues, the Grampians Group was considered as equivalent to Lower Devonian to Lower Carboniferous (Chapman 1917, footnote 2, Spencer-Jones 1965). The Grampians Group comprises predominantly non-marine quartzose sandstone, red siltstone and mudstone associated with basal acid volcanics of the Rocklands and Wickliffe Rhyolites. The

sediments are intruded by granite, granodiorite and associated sills and dykes. Recent isotopic dating of the granodiorite gave an age of Early to Middle Devonian (Vandenberg *et al.* 1976). The dates provided for the Mafeking Granodiorite, which intrudes the lowermost Red Man Bluff Sandstones (the sediments just below the Silverbank Formation), were at an average 381.5 million years, around those of the supposed Siluro-Devonian boundary and earliest Devonian (Spencer-Jones 1976).

The primary interpretation of the fish remains from Unit 3 of the Silverband Formation given here supports the evidence from radioactive dating; that is, the Grampians Group is of Early to Middle Devonian age and not younger. On balance the faunal evidence favours an Early Devonian age.

SYSTEMATIC PALAEONTOLOGY

"AGNATHA"

Subclass THELODONTI

Order THELODONTIDA

Family TURINIIDAE Obruchev 1964

Genus *Turinia* Traquair 1896

REMARKS: For discussion of the attributes of the scales of this genus see Gross (1967) and Karatajute-Talimaa (1978); for description of the type species, *Turinia pagei*, see Traquair (1899), Stensiö (1964), and Turner (1982b). *Turinia* is known from the latest Silurian in Greenland and possibly in the Welsh Borderland into the early Upper Devonian (Frasnian) in Australia.

Turinia fuscina sp. nov.

Figs 2 B-H, K-U

1963 Elasmobranch Dermal Denticles, Talent & Spencer-Jones, p. 10, fig. 4.

1982a turiniid thelodont, Turner, p. 117.

1984 *Turinia?* sp., Long & Turner, p. 235.

ETYMOLOGY: In allusion to the trident-like shape of the crowns of trunk scales.

DIAGNOSIS: Small to medium-sized thelodontid scales; rounded head scales with a high-peaked crown of up to 12 radiating ribs which may bifurcate at the crown rim; elongate transitional scales with large undulating ribs deeply dissecting the crown; and tripartite or monolithic trunk scales with a flat central area and a pair of lateral segments separated by a shallow groove, ending in sharp posterior points. Ventral crown ribs present in some

body scales. Shallow neck in all scales. Base relatively large and shallow in head and transitional scales. In trunk scales, the base is placed anteriorly and may be extended into a basal prong, or expanded laterally. Pulp canal may split into as many as three separate basal openings.

MATERIAL: Eighteen paratypes and possibly numerous other syntype scales embedded in samples of the Silverband Formation held in the Museum of Victoria, MV (NMV) "GSV" 54862-4, 8.

LOCALITY: 6a of Talent & Spencer-Jones (1963), table 2. REMARKS: All the scales are poorly preserved, white in colour and rather friable: many are cracked or broken. They are embedded in sandstone and can only be exposed by careful preparation with needles. No complete scales have been removed from the sediment and so it has not been possible to examine a scale 'in the round' or histologically. The figures represent parts of scales seen with the aid of the binocular microscope on the surface of the rock samples.

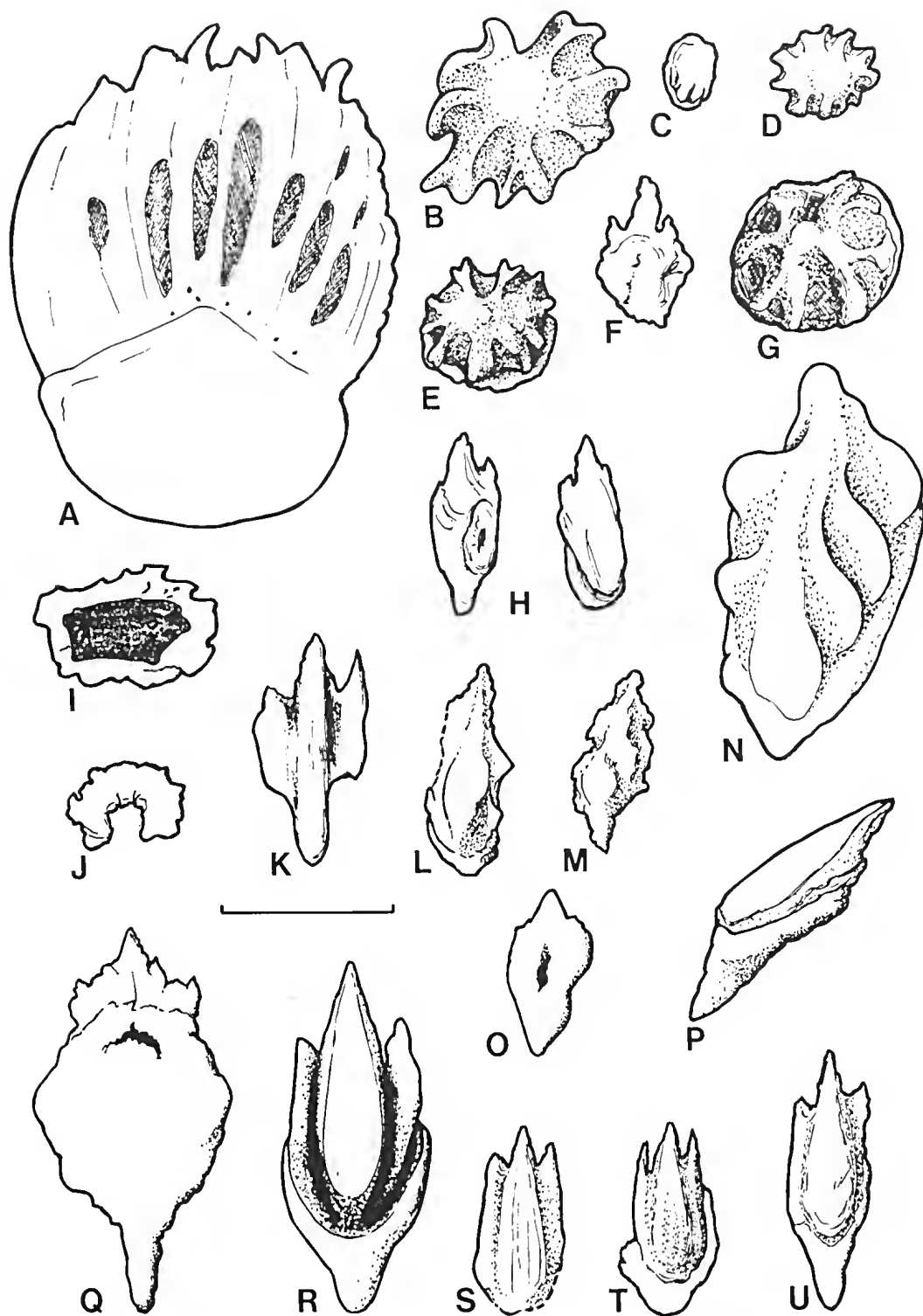
DESCRIPTION: The small scales are of the three main types typical of all thelodonts. There are rounded head scales, more elliptical transitional scales and lenticular and elongate trunk scales. Variations of the main types are thought to belong to special scales on the fins and tail, around the orifices and other small areas of the body.

Head scales are rounded and vary in length from 0.35-0.6 mm (fig. 2B, D, E, G). The overall shape of the crowns is dome-like. The crown rim is crenulated, with about 7 or 8 rounded ribs ascending towards the centre of the crown. These ribs can be bifurcated towards the crown rim so that a smaller number of ribs meets the smooth raised centre of the crown. The neck is low. The base is probably also low with a central pulp opening but this has not been observed in a head scale from the Silverband Formation. Smaller rounded scales, about 0.25 mm long, are probably special head or buccal scales (Fig. 2C).

Only one complete transitional scale has been observed (Fig. 2N). This is relatively large, 1.2 mm long, elliptical in outline with a high crown. There are rounded ribs ascending onto the relatively narrow top of the crown. The anterior rib is slightly bifurcate, and there are two or three ribs on either side merging into the posterior spur of the crown. The neck is low. The base is large and elliptical. There is one other poorly-preserved

Fig. 2—Devonian vertebrate microremains from the Silverband Fm., Grampians, western Victoria. A, I, Acanthodian? remains. A, Acanthodian? scale, *Gomphonchus* (*Poracanthodes*)? sp. horizontal section, NMV/54864.1. I, Acanthodian? spine in cross-section, NMV/54868.1. B-H, J-U, *Turinia fuscina* sp. nov. B, head scale, dorsal view, NMV/54864.2. C, head scale, dorsal view, NMV/54862.1. D, head scale, dorsal view, NMV/54862.2. E, head scale, dorsal view, NMV/54862a.1. F, body scale, ventral view, NMV/54863.1. G, head scale, dorsal view, NMV/54863.2. H, body scale, postero-lateral and dorsal views, NMV/54862.3. J, scale in cross-section, NMV/54868.2. K, body scale, dorsal view of crown, NMV/54862a.2. L, body scale, dorsal view, NMV/54862.4. M, transitional scale, NMV/54862.5. N, transitional scale, NMV/54862.6. O, base only, ventral view, NMV/54868.3. P, body scale, lateral view, NMV/54862.6. Q, body scale, ventral view, NMV/54862a.3. R, body scale, dorsal view, NMV/54862.7. S, body scale, dorsal view, NMV/54868.4. T, body scale, dorsal view, NMV/54862.8. U, body scale, dorsal view, NMV/54862.9.

Scale bar = 0.5 mm.



scale which is probably also a transitional scale (Fig. 2M).

Trunk scales observed range in size from 0.5 to 1.3 mm (Fig. 2F, H, L, P-Q, R-U). Those figured by Talent and Spencer-Jones (1963, fig. 4A-C) show the typical trident shape of the crown. Most have an elongate, tripartite crown with a raised central platform, which is flat (Fig. 2P, R, U) or slightly concave (Fig. 2S, T). Lateral segments are separated from the central area by a shallow trough (Fig. 2R, S, T). The lateral segments and the central area apparently elongate into three prominent posterior points, the central one being the longest (Fig. 2K?, R-U). One scale seen in lateral view is apparently devoid of lateral crown segments and has one short posterior rib descending onto the smooth neck (Fig. 2P). One or two scales seem to exhibit short curved riblets on the postero-ventral surface of the crown extending from the posterior crown points to abut on the neck-base line (Fig. 2H, Q). The neck is shallow and forms a distinct trough anterior to the crown rim. The base is large and can be expanded laterally (Fig. 2Q). The pulp opening is central or posteriorly-placed (Fig. 2H, O, Q) and can divide into as many as three separate openings (Fig. 2F). Several body scales exhibit short to long horizontal prongs on the anterior of the base (Fig. 2H, Q-R, U).

Broken scales (Fig. 2J-H) or scales preserved in basal view (Fig. 2O, Q) reveal histological features. They apparently agree with those of other turiniiform species (see e.g. Gross 1967, Turner & Dring 1981). The crown and neck are formed of simple orthodontine and the base is penetrated by one main pulp canal, which may split into a few basal openings.

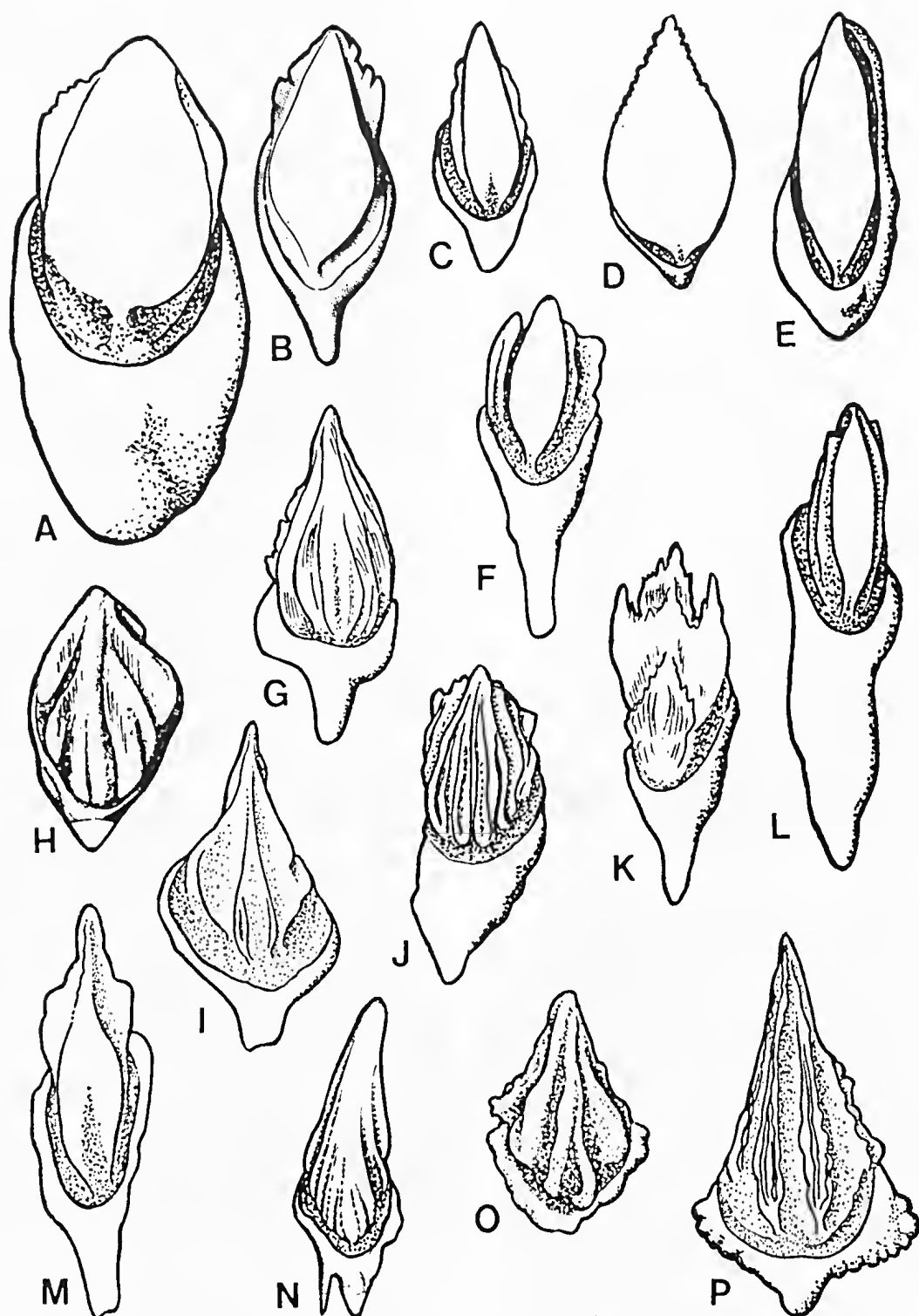
DISCUSSION

The scales referred here to a new species, *Turinia fuscina*, seem to be closest to the type *Turinia pagei* (Powrie 1870). The type species *sensu stricto* is found in latest Silurian (Upper Downtonian) to Siegenian in Europe and North America (Turner 1973, 1984). It has been recorded in Australia in the Devonian Cravens Peak Beds (Turner *et al.* 1981), although study of new material from the Georgina Basin suggests that some of the turiniid scales from the Cravens Peak Beds are better referred to a new species (Turner 1984).

The head and transitional scales seen in the Silverband Formation are very similar to all turiniiform and other thelodont head scales. Thelodonts and, for that matter, many shark groups have rounded head scales with undulating crown margins and radiating ribs. The crown ribs on the Silverband head scales do have a tendency to bifurcate and this character is seen in *Australolepis seddoni* Turner & Dring 1981 from the Frasnian Gneudna Formation and in some of the turiniid head scales from the Georgina and Amadeus material. The trunk scales, however, are more characteristic. These have flat monolithic central crown segments exactly like those in *Turinia pagei* and *Turinia polita* Karatajute-Talimaa 1978 which are found often in association in the Dittonian sediments of the Welsh Borderland, France and Podolia. The Silverband trunk scales differ in being noticeably tripartite. This feature is known, though not so extreme, in *T. pagei* scales. Scales similar to those of *T. pagei* and *T. polita* are also present in the Tumblong oolite of New South Wales which is considered to be Lower Devonian (Pickett *et al.* 1985); some of these scales are very like those of the new species.

The scales from the Silverband Formation are unlike the trunk scales of any contemporary or younger turiniiform scales as yet described—*T. australiensis* Gross 1971b from the Siegenian/Emsian and possibly younger of Australia (Turner *et al.* 1981, Turner 1982b), *Turinia* sp. nov. from the Georgina Basin and the Amadeus Basin (Young coll.), *Turinia* sp., "cf. *T. hutkensis*" from the Hatchery Creek Conglomerate Group of New South Wales (Eifelian/Givetian) (Young & Gorter 1981) and the Broken River Formation of Queensland (Turner 1984), *Turinia hutkensis* Blicek & Goujet (1978) from the Middle-Late Devonian of Iran, *Turinia* sp. nov. from the Broken River Formation of Queensland (Turner pers. obs.), *Turinia* sp. from the Arkaringa Basin of South Australia (Long, Young & Turner in prep.), *Turinia* spp. from the Middle Devonian of west Yunnan (Wang *et al.* in press), Antarctica (Turner & Young pers. obs.), and the Lower or Middle Devonian of Thailand? (Blicek *et al.* 1984), and South America (Goujet *et al.* 1984), and *Australolepis (Turinia?) seddoni* from the Gneudna Formation of Western Australia. All of these scales have more sculptured crowns with fine ribbing on the main

Fig. 3—Comparison of a selection of trunk scales from some of the known turiniid populations. A, *Turinia pagei* (Powrie 1870) Dittonian, Welsh Borderland (Turner coll.). B, *Turinia pagei* Dittonian, Podolia (from Karatajute-Talimaa 1978). C, *Turinia pagei* Dittonian, Welsh Borderland (Turner coll.). D, *Turinia polita* Karatajute-Talimaa 1978, Dittonian, Podolia (after Karatajute-Talimaa 1978). E, *Turinia polita* Dittonian, France (after Goujet & Blicek 1979). F, *Turinia fuscina* sp. nov. L? Devonian, Victoria (this paper). G, *Turinia australiensis* Emsian, Belvedere Formation, NSW (Pickett coll.). H, *Turinia australiensis* holotype, L. Devonian?, Western Australia (from Gross 1971b). I, *Turinia* sp. Emsian? Cravens Peak Beds, Georgina Basin, Queensland (after Turner *et al.* 1981). J, *Turinia hutkensis*, M. Devonian, Iran (after Blicek & Goujet 1978). K, *Turinia* sp. Cravens Peak Beds (after Turner *et al.* 1981). L, *Turinia pagei* Dittonian, Welsh Borderland (Turner coll.). M, *Turinia* sp. Cravens Peak Beds (after Turner *et al.* 1981). N, *Turinia* sp. M. Devonian, Hatchery Creek Conglomerate Group, NSW (after Young & Gorter 1981). O, *Australolepis seddoni* Turner & Dring 1981, Frasnian, Gneudna Formation, Western Australia (after Turner & Dring 1981). P, *Australolepis seddoni* Gneudna Formation (after Turner & Dring 1981). Not to scale: all turiniid thelodont scales depicted are within length range of 0.5-2.0 mm.



segments, extra lappets on the lateral segments, double ribs extending the full length of the crown, or ribs deeply dissecting the crown. Some even have small upturned hooks on the lateral crown/neck surface. A comparison of some *Turinia* trunk scales is shown in Fig. 3. The significance of these characters to the functional morphology or phylogeny of turiniiform thelodontids is not certain, but the wealth of new thelodont, especially turiniiform, material obtained in the last few years suggests that an analysis of all scale characters will prove helpful in understanding thelodont phylogeny. A preliminary study of such characters has been undertaken (Turner 1984) and will be presented in a future publication.

PISCES

OSTEICHTHYES?

Subclass ACANTHODII?

Family CLIMATIIDAE Berg 1940?

climatiid? cf. *Sinacanthus* P'an 1957

Fig. 2 1

1917 *Physonemus micracanthus* sp. nov. Chapman, pp. 84-84, pl. 5, figs 1-3.

1917 *Physonemus attenuatus* Davis; Chapman, pp. 85-86, pl. 5, fig. 4.

1917 *Physonemus* sp. Chapman, p. 86.

1957 *Physonemus?* *micracanthus* and cf. *Erismacanthus*, Baird, p. 1012.

1958 *Physonemus* (*P. attenuatus* and *P. micracanthus* Chapman, 1917), Hills, p. 91.

1963 '*Physonemus*' *micracanthus* Chapman, Talent & Spencer-Jones, p. 7, pl. 11, figs 4-8; fig 3.

1982 acanthodian spines, Turner, p. 117.

1984 acanthodian remains, Long & Turner, p. 237.

MATERIAL: See Talent and Spencer-Jones (1963). Ten specimens in the Museum of Victoria (P14363-5, P34318 type material, "GSV" 5447a-b, 13100, 57826, 57827).

LOCALITIES: 1, 2, 3, 4, 4a, 12 of Talent & Spencer-Jones (1963), table 2.

REMARKS: None of the fin spines is well-preserved and there are no signs of an unornamented shaft on any of them. This would seem to rule out the possibility that they are shark spines. The few specimens available resemble *Sinacanthus* spines found in various parts of China, where at least four species have been recorded from Silurian and Early Devonian sediments (P'an 1964, Liu 1973, P'an & Liu 1975, Li 1980, Wang *et al.* 1980). The Silverband spines seem very like those of *Sinacanthus triangulatus* P'an, Wang and Liu (1975) from the Lower Devonian of South China.

One specimen (Talent & Spencer-Jones 1963, pl. 11, fig. 7) is definitely more nodose than the others illustrated. This specimen might belong to a shark such as *Antarctilamna* Young (1982) and not to an acanthodian. *Antarctilamna* was a xenacanthiid shark from the Middle Devonian of Antarctica and New South Wales. However, the specimen also resembles the acanthodian spine form called *Neosiacanthus* by Wang *et al.* (1980). *Neosiacanthus* is found in association with *Sinacanthus* in the mid to Late Silurian Fentou Formation of east

China (Wang *et al.* 1980, Liu 1983). Other nodose climatiid(?) spines from the western MacDonnell Ranges of the Amadeus Basin are discussed and figured by Young (1985, fig. 81); these came from the Harajica Sandstone Member of the Parke Siltstone which Young considered to be of Givetian to Frasnian age.

Family ISCHNACANTHIDAE Berg 1940?

Genus *Gomphonchus* Gross 1971?

Gomphonchus? sp.

Fig. 2A

1963 Elasmobranch Dermal Denticles, Talent & Spencer-Jones, p. 10.

1963 Elasmobranch Teeth, Talent & Spencer-Jones, p. 10, pl. 11, fig. 2, 3, 8.

1982 acanthodian tooth whorls, Turner, p. 117.

1984 cf. *Paracanthodes*, Long & Turner, p. 240 (*Paracanthodes*, in error).

MATERIAL: Two scales and three tooth whorls noted so far in rock samples housed in the Museum of Victoria ("GSV" 58218-9, 54862, 54864, 54868).

LOCALITIES: 2, 3, 6a of Talent & Spencer-Jones (1963), table 2.

REMARKS: Gross (1957, 1971) studied acanthodian tooth whorls in great detail. He showed that some climatiids such as *Nostolepis* had tooth whorls with flattened transverse blades whereas those of the ischnacanthids such as *Gomphonchus* had stabbing cusps.

Some other Devonian fishes (onychodontid cross-opterygians and, perhaps, some early sharks) also possessed tooth whorls and cannot be ruled out as the source of the Silverband specimens. However, the tooth whorls figured by Talent and Spencer-Jones appear very like ones referred to *Gomphonchus* (Gross 1957, Denison 1979).

Two large scales, one figured (Fig. 2A), are seen in natural horizontal section. These are very similar to those called *Paracanthodes*, which Gross (1957) thought were special lateral line scales of *Gomphonchus*. However the possibility that these larger scales are those of a shark, *Antarctilamna* (Young 1982) for example, cannot be ruled out until more Silverband scale material is available for study and until scales of that shark genus are examined histologically. One scale seen on slab 54868 has a crown of curved angled ribs like those of the trunk scales of *Antarctilamna* portrayed by Young (1982, pl. 87, figs 6-7).

Discovery of acanthodian jawbones, for example, in the Silverband Formation would help to resolve the identification with more certainty. Scales, spines and teeth of climatiids and ischnacanthids of *Nostolepis* and *Gomphonchus* types are found elsewhere in the Upper Silurian and Lower Devonian of Australia (Long & Turner 1984). These forms are not known in sediments younger than Siegenian.

SUMMARY OF SILVERBAND FAUNA

On the one hand the Silverband Formation fauna can be interpreted as follows:

Agnatha: Thelodonti *Turinia fuscina* sp. nov.

Osteichthyes: Acanthodii ischnacanthiid *Poracanthodes/Gomphonchus* sp. climatiid? cf. *Sinacanthus*

This interpretation of the fauna appears to me to be the most likely assessment based on the morphology of the turiniid scales and the association of the thelodont and acanthodian remains. It supports a Lower Devonian age for Unit 3 of the Silverband Formation.

If, however, it could be confirmed that the fin spines, tooth whorls and larger scales derive from sharks such as *Antarctilamna* Young 1982, or from acanthodians such as those found in the Amadeus Basin (Young 1985), then the Silverband Formation is younger, possibly late Middle Devonian or early Frasnian. This would mean that *Turinia fuscina* is one of the youngest thelodont species. Turiniids are known to be associated with sharks in the late Middle Devonian of Antarctica (Young & Turner pers. obs.). The presence of turiniiform thelodont scales puts an upper limit of early Frasnian and a lower limit of late Pridolian/early Gedinian on the Silverband Formation.

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A NEW SPECIES OF GREEN TREE FROG (ANURA: HYLIDAE) FROM QUEENSLAND, AUSTRALIA

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ABSTRACT: The nominal species of hylid frog *Litoria chloris* (Boulenger) is demonstrated to include two species. *Litoria chloris sensu stricto* occupies coastal localities in southeastern and south-central Queensland and northern New South Wales, and an allopatric population in northern coastal Queensland is here described as *L. xanthomera* sp. nov. It is distinguished by external morphology as well as by estimates of genetic distance derived from isoenzyme electrophoresis. Osteology, larval form and male call are described.

The known frog fauna of Australia has increased exponentially over the last decade (Tyler 1982). A major contributing factor has been access to the monsoonal wet-dry tropics of the north of the continent during the wet season when fossorial species are active. Concurrently, knowledge of the fauna of the north-eastern seaboard of Australia has improved, principally as a result of a comprehensive faunal survey program by the Queensland National Parks and Wildlife Service.

Davies and McDonald (1979) examined the morphology of three disjunct populations of the hylid frog *Litoria chloris* (Boulenger), and noted differences between the northern population and the other two populations (southern and central) in the eye and thigh colouration and head length to head width ratios. They did not assign specific status to the northern population in the absence of call and life history data.

A preliminary electrophoretic survey of a number of species of Australian hylids (Adams, unpublished) indicated that genetic differences existed between the northern and southern populations of *L. chloris*. This paper includes a comprehensive electrophoretic study of *L. chloris* and confirms the genetic uniqueness of the northern population. In the light of this information and with the availability of call and life history data we herein describe the northern population as a new species.

MATERIALS AND METHODS

ELECTROPHORESIS

A total of 21 specimens from four populations derived from the three geographic areas was available for electrophoresis. The northern form was represented by two samples. Sample D was collected in 1981 and the tissues obtained were found to be still suitable for electrophoretic analysis. The other three samples were collected in February, 1984. Reference material is deposited in the South Australian Museum, Adelaide (SAM): *Northern Population*, SAM R25736-40, Lancelot State Forest, K.R. McDonald and P. Minton (Sample C); *Central Population*, SAM R25761-66, Eungella, N.P., Qld, K.R. McDonald (Sample B);

Southern Population, SAM R25758-60, Watagan S.F., N.S.W., M. Mahony (Sample A). Sample D (northern population) was from Caithu State Forest, Qld.

Liver from each specimen was homogenized in an equal volume of lysing solution (distilled water containing 10 mg NADP and 0.1 ml β mercaptoethanol per 100 ml). Homogenates were then centrifuged at 10,000 g for 10 minutes at 4°C and the supernatants stored at -20°C in separate 5 μ l aliquots.

Electrophoresis was conducted according to standard techniques as described in Baverstock, Watts, Adams and Gelder (1980). The proteins of an estimated 43 loci gave sufficient activity and resolution to be scored. The proteins stained, together with the abbreviations used and the appropriate Enzyme Commission number, are:

Aconitase (ACON: 4.2.1.3), Acid phosphatase (ACP: 3.1.3.2), Adenosine deaminase (ADA: 3.5.4.4), Adenyl kinase (AK: 2.7.4.3), Albumin, (ALB), Carbonic anhydrase (CA: 4.2.1.1), Diaphorase (DIA: 1.6.2.2), Enolase (ENOL: 4.2.1.11), Fumarase (FUM: 4.2.1.2), Glyceraldehyde-3-phosphate dehydrogenase (GA3PD: 1.2.1.12), Glutamate-oxaloacetate transaminase (GOT: 2.6.1.1), α Glycerophosphate dehydrogenase (α GPD: 1.1.1.8), Glucose-phosphate isomerase (GPI: 5.3.1.9), Glutathione reductase (GSR: 1.6.4.2), Guanylate kinase (GUK: 2.7.4.8), Glyoxalase I (GLO I: 4.4.1.5), Isocitrate dehydrogenase (IDH: 1.1.1.42), Lactate dehydrogenase (LDH: 1.1.1.27), Malate dehydrogenase (MDH: 1.1.1.37), Malic enzyme (ME: 1.1.1.40), Mannose-phosphate isomerase (MPI: 5.3.1.8), Peptidases (PEP (A, B, C, D): 3.4.11 or 13), Phosphoglycerate mutase (6PGD: 2.7.5.3), 6 Phospho-gluconate dehydrogenase (6PGD: 1.1.1.44), Phosphoglycerate kinase (PGK: 2.7.2.3), Phosphoglucomutase (PGM: 2.7.5.1), Pyruvate kinase (PK: 2.7.1.40), Superoxide dismutase (SOD: 1.15.11), Sorbitol dehydrogenase (SORDH: 1.1.1.14), Triose-phosphate dehydrogenase (TPI: 5.3.1.1).

Genetic distances between populations were calculated as fixed differences or as Nei differences corrected for small sample sizes (Nei 1978).

MORPHOMETRIC ANALYSIS

The specimens reported here are deposited in institutions abbreviated in the text as follows: American

TABLE 1

ALLELE FREQUENCIES AT 43 LOCI IN THE FOUR POPULATIONS OF *Litoria chloris*. Populations A-D as in Davies & McDonald (1979). Alleles are designated a, b, c, etc. in order of increasing electrophoretic mobility. Where there is more than one locus scorable per enzyme, loci are numbered in order of increasing electrophoretic mobility

		Southern	Central	Northern	
		A	B	C	D
<i>Acon-1</i>	b	100	100	100	64
	a				36
<i>Acon-2</i>	c		83		
	b		17	100	100
	a	100			
<i>Ada-2</i>	c		58		
	b	100	42		
	a			100	100
<i>Ak-1</i>	b		42	60	36
	a	100	58	40	64
<i>Ca</i>	b	100	75	100	100
	a		25		
<i>Dia-1</i>	b	100	100		
	a			100	100
<i>Enol</i>	b	50	50	40	50
	a	50	50	60	50
<i>Fum</i>	b	100	100		
	a			100	100
<i>Ga₂pd</i>	b		100	60	100
	a	100		40	
<i>Got-2</i>	b	100	100	90	100
	a			10	
<i>αGpd</i>	b			100	100
	a	100	100		
<i>Gpi</i>	b	50	100	100	100
	a	50			
<i>GloI</i>	b	100	100	80	100
	a			20	
<i>Ldh-2</i>	b	83	100	100	100
	a	17			
<i>Me-2</i>	b	100	42	100	100
	a		58		
<i>Mpi</i>	b			100	100
	a	100	100		
<i>Pep B</i>	c		17		
	b		83		
	a	100		100	100
<i>Pep C1</i>	b	50	92		
	a	50	8	100	100
<i>Pep C2</i>	b	100	40		
	a		60	100	100
<i>Pep D</i>	e				50
	d		17		
	c		8		
	b	100	75	50	40
	a			50	10
<i>6Pg_d</i>	c		25	100	100
	b	100	67		
	a		8		
<i>Pgm-1</i>	b		8		
	a	100	92	100	100
<i>Pgm-2</i>	c			100	100
	b	100	92		
	a		8		
<i>Pk</i>	b		40	80	100
	a	100	60	20	

TABLE 1 continued

		Southern A	Central B	C	Northern D
<i>Sod</i>	b			100	100
	a	100	100		
<i>Sordh</i>	c				15
	d		8	60	64
	c	50		20	7
	b	50	92	10	7
	a			10	7
<i>Tpi</i>	b		100		50
	a	100		100	50

The following 16 loci were invariant: *Acp*, *Ada-1*, *Ak-2*, *Alb*, *Dia-2*, *Got-1*, *Gst*, *Guk*, *Idh-1*, *Idh-2*, *Ldh-1*, *Mdh-1*, *Me-1*, *Pep A*, *Pgam*, *Pgk*.

Museum of Natural History (AMNH); Australian Museum, Sydney (AM); British Museum (Natural History) (BMNH); Museum of Comparative Zoology, Harvard (MCZ); University of Kansas, Museum of Natural History (KU); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAM); Western Australian Museum, Perth (WAM).

Methods of measurement follow Tyler (1968) and osteological descriptions follow Trueb (1979). Tadpoles were fixed in Tyler's (1962) fixative and staged according to Gosner (1960). Osteological specimens were cleared and stained for bone after Davis and Gore (1947) and for bone and cartilage after Dingerkus and Uhler (1977). Measurements were made using dial calipers or an eyepiece micrometer. Measurements of adults were: snout to vent length (S-V); tibia length (TL); head length (HL); head width (HW); eye to naris distance (E-N); internarial span (IN); eye diameter (E); tympanum diameter (T). The following ratios were calculated: TL/S-V; HL/HW; HL/S-V; E-N/IN. Where appropriate, means \pm standard deviations followed by ranges are given.

Calls were recorded using a Uher 4000 tape recorder with Grampian DP4 or AKG D190 ES dynamic microphones. Dry bulb air temperatures were measured with a Shultheis quick reading thermometer close to the calling sites of males. Calls were analysed by means of a sound spectrograph (Kay Digital Sona-Graph-7800). Temporal characteristics of the calls were determined from wideband (300 Hz bandpass) and spectral characteristics from narrowband (45 Hz bandpass) spectrograms. Three examples of each call from each male were analysed and mean values calculated.

RESULTS

ELECTROPHORESIS

The results of the electrophoretic analysis are shown in Table 1 as putative allele frequencies for each population at 43 presumed gene loci. Table 2 gives the genetic distance estimates between populations. The two populations of the northern form of *Litoria chloris* are genetically similar (0% fixed differences; Nei D of 0.017). In contrast, the northern form differs markedly from both the southern and central populations (average fixed difference, 23%; average Nei D, 0.379). There is some genetic differentiation between the central and southern populations (9% fixed difference; Nei D, 0.152).

MORPHOMETRIC ANALYSIS

Davies and McDonald (1979) analysed morphological variation between the three allopatric populations of *L. chloris* and showed that the head length to head width ratio of the northern population is statistically significantly different from that of the other two populations.

The northern population is distinctive in having orange thighs as opposed to blue thighs in the other two groups and in having an orange rim to the eye rather than a red rim as found in central and southern populations.

ADVERTISEMENT CALL

Audiospectrograms of calls of specimens from the northern and southern populations are shown in Fig. 1, and call parameters are listed in Table 3. It can be seen that there is overlap of pulse repetition rates between the

TABLE 2
GENETIC RELATIONSHIPS AMONG POPULATIONS OF *Litoria chloris*. Percentage fixed differences are shown below the diagonal with corrected Nei D's above.

		A	B	C	D
Southern	A	0			
Central	B	9	0		
Northern	C	23	21	0	
Northern	D	28	20	0	0

TABLE 3
PHYSICAL CHARACTERISTICS OF CALLS OF MALES OF *Litoria xanthomera* AND *L. chloris*. Mean values are given with ranges in parentheses.
P.R.R. = pulse repetition rate.

Species, locality & date	Dry bulb temp. °C	Duration msec	No. of pulses	P.R.R. pulses/sec	Dom. Frequency Hz
<i>L. xanthomera</i> Henrietta Ck, Palmerston N.P. 13 Feb 1980 (Holotype)	21.8°C	76.67 (63-84)	162.33 (152-174)	217 (181-276)	2900
<i>L. xanthomera</i> type locality, 13 Feb 1980	21.8°C	61.67 (60-63)	158.67 (148-165)	257 (247-266)	3000
<i>L. xanthomera</i> Crater N.P. 13 Feb 1977	21.8°C	97.17 (93-99.5)	183.67 (174-192)	189 (187-193)	2900 3100
<i>L. chloris</i> Sunday Ck 23 Oct 1976	19.7°C	60.33 (60-61)	124 (119-128)	205 (198-210)	2600
<i>L. chloris</i> Kilcoy Ck 17 Oct 1978	17.2°C	83 (82-84)	120.33 (118-123)	145 (144-146)	2500

two groups and this rate would be expected to be more similar at comparable temperatures. Differences are apparent in pulse number and dominant frequency.

DISCUSSION

The present study has demonstrated extensive genetic divergence between the northern and southern forms (populations A and B) of *L. chloris* but has not demonstrated significant divergence in the male call characteristic of the two populations. Divergence in colour and in head shape has been noted previously (Davies & McDonald 1979).

The level of genetic divergence encountered far exceeds that typically found between populations of the same species (Avisé 1974; Ayala 1975; Baverstock *et al.* 1977, 1980, 1982, 1983; Case 1978; Avisé & Aquadro 1982; Adams unpublished). The degree of similarity between the southern and central populations, on the other hand, is consistent with that typical of allopatric populations of a single species.

It is not known how long the populations of *L. chloris* have been isolated, but clearly substantial divergence has occurred. The lack of significant divergence in call structure raises doubt as to the recognition of the northern form as a separate species. However, the genetic data are consistent with there being two species within *L. chloris* as currently recognised. Coupled with the morphological and phenotypic differences recorded, these considerations lead us to recognise the northern form of *L. chloris* as a separate species.

Litoria xanthomera sp. nov.

Figs. 1-9

Hyla chloris: Moore 1961, p 263 (part.)

Litoria chloris: Davies & McDonald 1979, p 353 (part.)

HOLOTYPE: QM J42011, an adult male from Henrietta Creek, Palmerston National Park, Qld, Australia (17°37', 145°40') collected on 13 Feb. 1980 by K.R. McDonald.

PARATYPES: SAM R24529-39, WAM R82619-20, KU 193847-48, BMNH 1983. 910-911, AM R106905-6, AMNH 117640-41, MCZ 106117-18 collected with the holotype; QM J17109, Atherton, Qld (17°16', 145°29') I.R. Straughan, 22 Feb. 1961; QM J17110, Crystal Cascades, via Cairns (145°40', 16°58') 15 Jan. 1965; QM J27105-6, Little Forks, S of Shiptons Flat, Qld (145°14', 15°48'30") G.J. Ingram, 16-21 Nov. 1975; QM J25194-5, Home Rule Falls, Cooktown (15°28', 145°15') J. Covacevich and T. Tebbble, 28 Oct. 1974; QM J25258-60, Home Rule Falls, 30 km S Cooktown (15°28', 145°15') J. Covacevich and T. Tebbble, 28 Oct. 1974; QM J25278, 0.4 km E of the Granites, Home Rule, 30 km S of Cooktown (15°28', 145°15'), J. Covacevich and K.R. McDonald, 16 Nov. 1974; QM J38900, 33910, Crater N.P., (17°26', 145°29'30"), K.R. McDonald and R.G. Atherton, 13 Feb. 1977; QM J35901-3, 35950, 36011, NPWS Base, Palmerston N.P. (17°36', 145°46') K.R. McDonald and R.G. Atherton, 11 Feb. 1977; QM J35916, 35985, Mt Lewis State Forest (16°35', 145°16') K.R. McDonald and R.G. Atherton, 15 Feb. 1977; QM J35919, 35986, McDowell Ra. (16°06', 145°20'), R.G. Atherton and J.W. Winter, 21 Oct. 1976; QM J35921, 39963, 36024 Lake Barrine N.P., (17°15', 145°38'), J. Winter, 5 March, 1973; QM J35943, 35960, Severin Boar Pocket, Atherton Tablelands (17°11'S, 145°40'E), J. Winter, 21 Oct. 1975; QM J35944, 35946, Mt Baldy, 7 km SW Atherton (17°19', 145°25') J. Winter and R. Atherton, 28 Nov. 1976; QM J35962, 36020, Longlands Gap, J. Winter, 1 Feb. 1973; SAM R16794-8 Gadgarra, S.F. (145°40',

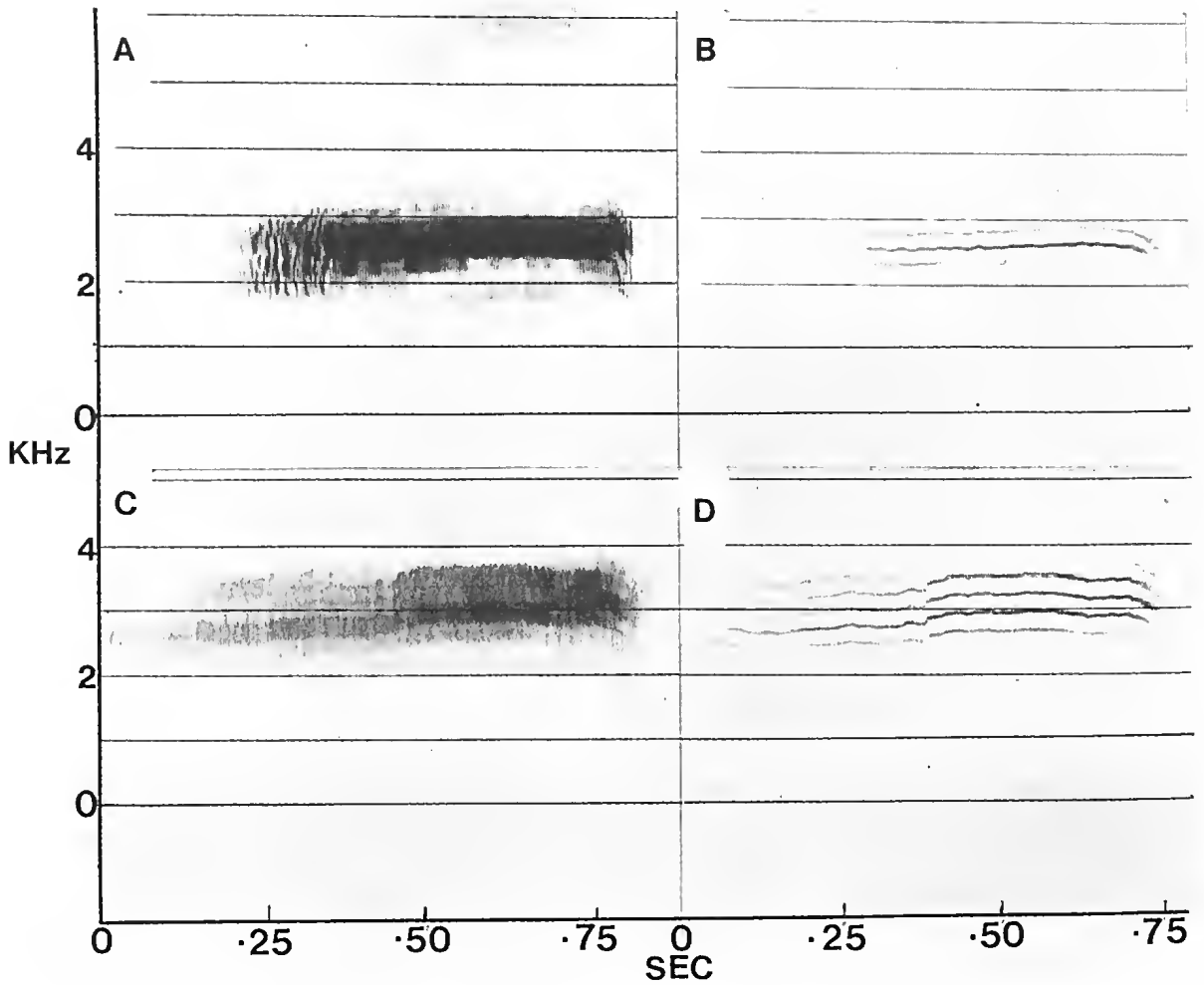


Fig. 1—Audiospectrograms of calls. A, B, *Litoria chloris* (Sunday Creek, Conondale Ra., Qld), A, 300 Hz bandpass, B, 45 Hz bandpass; dry bulb 17.2°C. C, D, *Litoria xanthomera* (holotype), C, 300 Hz bandpass, D, 45 Hz bandpass; dry bulb 21.8°C.

17°16'30") K.R. McDonald and R.G. Atherton, 14 Feb. 1977; SAM R24524-5 (Cleared and stained) Gadgarra S.F. (145°40', 17°16'30"), K.R. McDonald and R.G. Atherton, 14 Feb. 1977; SAM R24526, Milaa Milaa Falls, 2 km from Milaa Milaa (145°37', 17°30') K.R. McDonald and R.G. Zweifel, 16 Jan. 1981; SAM R24528 Kuranda S.F., 2.6 km along Black Mt Road from Kuranda, (145°38'30", 16°48') 24 Oct. 1981. K.R. McDonald, R.G. Zweifel and W. Hosmer; SAM R24529, nr Pearamon, (145°27'30", 17°19'), K.R. McDonald and R.G. Zweifel, 18 Jan. 1981. SAM R25736-40, Lannereost S.F., nr Wallamin Falls, K.R. McDonald and P. Minton, 16 Feb. 1984.

DIAGNOSIS: A moderately large green species (females 43-55 mm, males 40-56 mm) with widely expanded finger and toe discs, well developed finger and toe webbing, orange rimmed eyes, brilliant orange thigh markings and a rounded canthus rostralis.

DESCRIPTION: Head flattened, slightly broader than long (HL/HW 0.99); head length about two-thirds of

snout to vent length (HL/S-V 0.32). Snout not prominent, truncate when viewed from above (Fig. 2), abrupt, very slightly rounded in profile (Figs. 3, 4). Nostrils lateral, distance from end of snout about 25% that from eye. Eye to naris distance less than internarial span (E-N/IN 0.85). Canthus rostralis well defined and slightly curved. Eye large, extremely prominent (Fig. 4), diameter greater than eye to naris distance. Tympanum distinct, covered with skin, diameter less than eye diameter, separated from eye by distance about 50% own diameter. Vomerine teeth in two small series, close together, angled at about 45° to midline between and below choanae. Tongue moderately large, triangular.

Fingers short with lateral fringes. Order of length $3 > 4 > 2 > 1$ (Fig. 5A). Webbing between 3 and 4 reaches subarticular tubercles at base of penultimate phalanx on 4. Terminal discs prominent with well developed circummarginal grooves. Hind limbs moderately long and slender (TL/S-V 0.54). Toes in order of length $4 > 5 > 3 > 2 > 1$. Webbing between 1 and 2

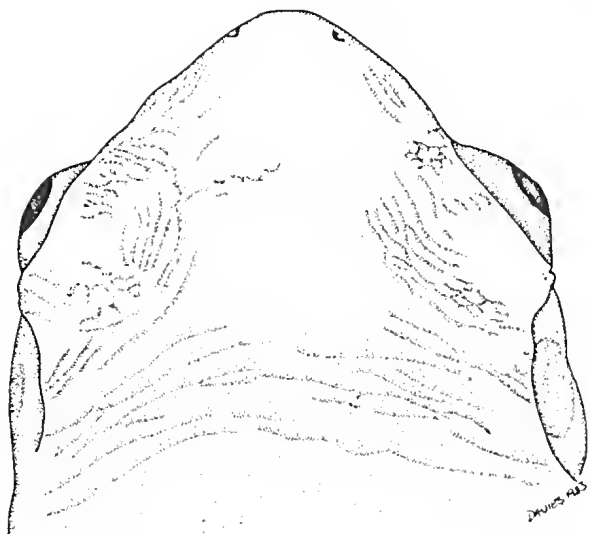


Fig. 2—Dorsal view of head of holotype of *Litoria xanthomera*. QM J42011.

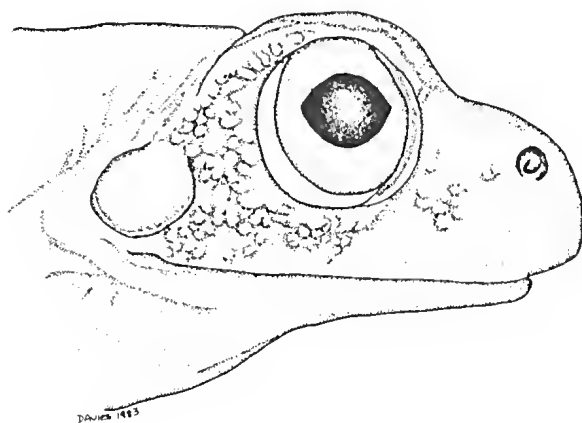


Fig. 3—Lateral view of head of holotype of *Litoria xanthomera*. QM J42011.



Fig. 4—*Litoria xanthomera* in life. Specimen from Palmerston National Park, Qld.

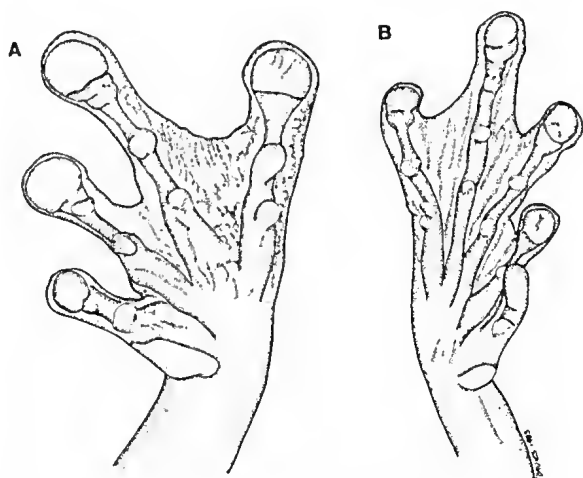


Fig. 5—A, Palmar view of hand and B, plantar view of foot of holotype of *Litoria xanthomera*. QM J42011.

from disc to subarticular tubercle on penultimate phalanx of 2, the same between 2 and 3, and 3 and 4, and from subarticular tubercle on penultimate phalanx of 4 to disc of 5 (Fig. 5B). Small oval inner and no outer metatarsal tubercle.

Dorsal and lateral surfaces of head and body finely granular. Inconspicuous dermal fold at wrist. Prominent slightly curved supratympanic fold from eye to level of forearm insertion. Throat and chest smooth, abdomen and thighs granular.

No nuptial pad developed. Submandibular vocal sac.

COLOURATION: *In preservative* — Dorsum, side of head and body, forearm, dorsal surface of tibia and medial dorsal stripe on tarsus, blue. Ventral surface, fingers, toes, upper portion of arm and thighs pale cream. Ventral surface cream. *In life* — Brilliant lime green on

dorsum, lateral head and body, forearm, dorsal surface of tibia and medial dorsal stripe on tarsus. Dorsal surface of forearm yellow. Throat, ventrolateral surface of body yellowish/orange, thighs brilliant orange, ventral surface yellow. Eye rim bright orange.

MEASUREMENTS OF HOLOTYPE IN MM: S-V 44.1; TL 24.0; HL 14.3; HW 14.5; E-N 3.4; IN 4.0; E 4.9; T 3.2 **VARIATION:** Adult males measure 40.3–55.7 mm S-V and females measure 43.1–55.9 mm (47.74 ± 3.83 , 40.3–55.9). Hind limbs moderately long (TL/S-V $0.54 \pm .02$, 0.50–0.58). Head length longer than head width (HL/HW 1.04 ± 0.44 , 0.93–1.11). Head length about 33% snout to vent length (HL/S-V $0.33 \pm .02$, 0.29–0.35). Eye to naris distance to internarial span ratios highly variable (E-N/IN 0.98 ± 0.14 , 0.77–1.27).

There is little or no variation in finger and toe webbing. In one specimen the tympanum is indistinct. Variability in colouration includes commonly a thin green stripe along the upper surface of the thigh (Fig. 4). In many specimens green colouration extends along the lateral edges of toe 5 and finger 4 and in some specimens along the lateral edge of toe 4 as well. Green colouration of the dorsal surface of the discs of toe 5 and finger 4 is detectable in some specimens.

Three of the paratypes have bulges beneath the dorsal skin behind the tympanum. These are attributed to the presence of larvae of dipteran (batrachomyid) parasites.

OSTEOLOGY: Skull moderately robust with moderately well ossified neurocranium (Fig. 6). Sphenethmoid well ossified extending between but not anteriorly to nasals dorsally and between vomers ventrally; overlapped dorsolaterally by nasals. Prootic completely fused with exoccipital; exoccipitals confluent. Crista parotica well developed, short, stocky, not articulating laterally with moderately expanded otic ramus of squamosals. Frontoparietal fontanelle moderately extensive, overlapped posterolaterally by moderately slender frontoparietals

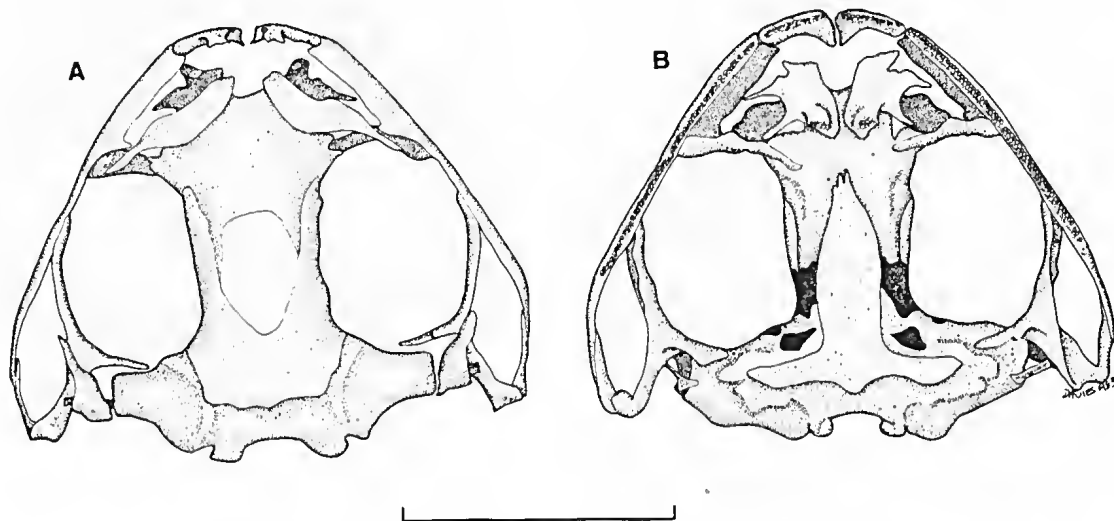


Fig. 6—A, Dorsal and B, ventral view of skull of *Litoria xanthomera*. SAM R24524. Scale bar = 10 mm.

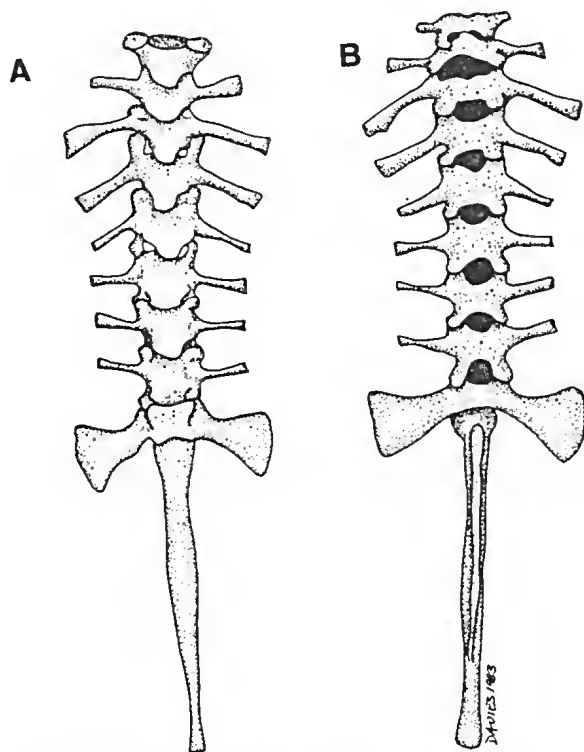


Fig. 7—A, Dorsal and B, ventral view of vertebral column of *Litoria xanthomera*. SAM R24524.

which extend about 67% of length of orbit. Anterior margin of frontoparietal fontanelle formed by sphenethmoid at level slightly less than anterior third of length of orbit. Posterior margin at level of anterior extremities of epiotic eminences. Nasals slender, moderately separated medially with slender acuminate maxillary processes not articulating with well developed preorbital processes of deep pars facialis of maxillaries (Fig. 6A). Palatines moderately long, ridged posteriorly (Fig. 6B), slightly tapering medially to terminate on sphenethmoid at level of lateral extremities of vomerine teeth. Parasphenoid robust with broad cultriform process, acuminate anteriorly, with short slender alary processes at right angles to cultriform process, not overlapped laterally by medial arms of pterygoid.

Pterygoid robust, anterior arm in short contact with palatal shelf of maxillary at level about $\frac{2}{3}$ anteriorly on length of orbit; medial arm moderately long. Quadratojugal entire and in long contact with maxillary. Squamosals robust with short zygomatic rami. Maxillary and premaxillary dentate. Alary processes of premaxillaries broad, inclined slightly posteriorly. Palatine processes of premaxillaries well developed, not quite articulating medially. Vomers entire; alac form anterior and medial margins of choanae (Fig. 6B). Dentigerous processes short, bearing seven teeth, angled slightly to

midline. Bony columella present. Hyoid plate very short, width about double length; alary processes absent; posterolateral processes long and tapering.

Pectoral girdle arciferous and robust. Omosternum and xiphisternum present; clavicles slender, curved, moderately separated medially; coracoids robust, widely separated medially. Bicapitate scapula slightly longer than clavicles. Suprascapula about $\frac{1}{2}$ ossified. Humerus with poorly developed dorsal crest. Eight procoelous nonimbricate presacral vertebrae. Relative widths of transverse processes $\text{III} > \text{IV} > \text{V} > \text{VI} > \text{II} = \text{VII} \approx \text{VIII}$ (Fig. 7). Sacral diapophyses moderately expanded, ilia extend half way along their length. Urostyle bicondylar with dorsal crest extending about $\frac{2}{3}$ its length. Pubis ossified; poorly developed dorsal prominence on ilium, rounded dorsal protuberance more superior than lateral.

Phalangeal formula of hand 2, 2, 3, 3. Terminal phalanges clawed. Well developed bony prepollex. Phalangeal formula of foot 2, 2, 3, 4, 3; small ossified prehallux. Intercalary structures cartilaginous.

LARVAE: The mouth disc (Fig. 8) has a formula of $\frac{1}{1} \frac{1}{2} \frac{1}{1}$ (see Martin 1965) and a well developed horny beak.

The papillary border is well developed and extends around the sides and back of the mouth disc. A larva at stage 40 is shown in Fig. 9. Larvae are poorly pigmented, and tail fins are shallow. The spiracle is sinistral and below the midline, and the anus opens dextrally. Larvae are indistinguishable from those of *Litoria chloris* (see Watson & Martin 1979).

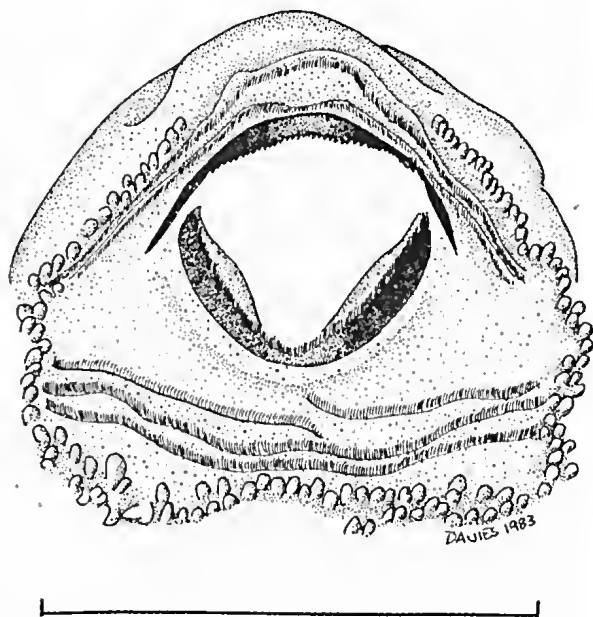


Fig. 8—Mouth disc of stage 40 larva of *Litoria xanthomera*. Scale bar = 2 mm.

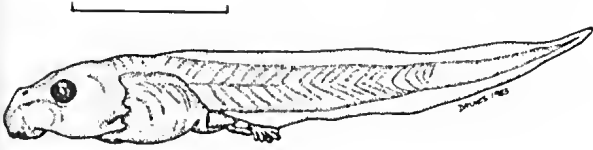


Fig. 9—Lateral view of larva, Stage 40, of *Litoria xanthomera*.
Scale bar = 10 mm.

CALL: Audiospectrograms of male calls of *L. xanthomera* and *L. chloris* are shown in Fig. 1 and call parameters are listed in Table 3. The call is a long growl at a dominant frequency of about 3000 Hz.

ETYMOLOGY: The specific name is derived from *xanthos* (Gk), "orange" and *meros*, "thigh" in reference to the colour of the thighs of this species.

DISTRIBUTION: Davies and McDonald (1979) mapped the distribution of this species as the northern population of *L. chloris*. The frog is confined to coastal rainforest from Home Rule to Mt Halifax in Queensland (McDonald unpubl.).

COMPARISON WITH OTHER SPECIES: *Litoria xanthomera* differs from all Australian congeners other than *L. gracilentia* and *L. chloris* in its size and brilliant green colouration. *Litoria gracilentia* is a smaller frog (males 31-42 mm and females 32-45 mm), with mauve thighs and a clearly defined, straight canthus rostralis. *Litoria xanthomera* is most closely related to *L. chloris* from which it differs in its brilliant orange thighs (blue in *L. chloris*), orange rimmed eye (red in *L. chloris*), head length to head with ratios (Davies & McDonald, 1979) and liver enzymes.

ACKNOWLEDGEMENTS

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THE VEGETATION ECOLOGY OF A COASTAL SAND DUNE IN SOUTH-EASTERN AUSTRALIA: GUNNAMATTA BEACH

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ABSTRACT: The vegetation of Gunnamatta Beach, Victoria, is described in a series of topographic/vegetation units that generally agree with a numerical classification. Probable successional sequences are postulated, but spatial pattern appears to be determined largely by disturbance and concomitant erosion. Of the soil factors investigated only soil organic matter content seemed to coincide with the vegetation pattern; no correlation with salt spray was observed.

Ecological studies on coastal sand dune plants in Australia have received surprisingly little attention, although sand dunes cover a sizeable proportion of the long coastline. What studies there are have concentrated on only a few aspects (Osborn 1922, Patton 1934, Burges & Drover 1953, Smith 1957, Turner, Carr & Bird 1962, Parsons 1966, Parsons & Gill 1968, Harty & McDonald 1972, Robin & Parsons 1976, Batianoff & McDonald 1980, Moore 1980, Barson & Calder 1981). This present work is a local synthetic study of vegetation pattern, soil characteristics, succession and more importantly the habitat factors which apparently influence species distribution (Sacheti 1983). The work was carried out on a dune complex at Gunnamatta Beach, Victoria.

STUDY AREA

Situation

Gunnamatta Beach (Fig. 1) forms the south-eastern part of the Nepean Peninsula (lat. 38°25'S. long. 144°48'E). This Peninsula covers about 72 km² of mainly dune material. It lies between King Bay (Bass Strait) on the south and Port Phillip Bay on the north, its western extremity being Pt Nepean. In the east it extends to the scarp of Selwyn Fault, near Cape Schanck (Keble 1968). The front dunes of this beach run approximately south-east, parallel to the coast.

Geology and Geography

The Nepean Peninsula now consists largely of hummocky dune terrain, with some active dunes and others which are relatively stable beneath vegetation (scrub, woodland or grassland). The sand of these superficial Holocene dunes is mainly calcareous with about 25% quartz (Keble 1968); underneath there are Pleistocene dune sandstones. The present topography of Gunnamatta Beach is that of highly complex dunes whose irregularity is partly the result of past disturbances and more recently intensive recreational use.

History

Some evidence suggests that the study area was once covered by woodland—probably *Casuarina*, *Eucalyptus* and *Acacia* (Powell 1967). Aborigines of the Bunurung tribe inhabited this part of Victoria and it has been sug-

gested that they used different plant parts for food (Brough Smyth 1878, Keble 1928) and used fire for cooking and hunting. Bird (1975) has remarked that natural vegetation was probably altered by the fires set by the aborigines whose kitchen middens can still be seen along the shores of the Nepean Peninsula. At Gunnamatta, some middens are on the mouth of the big blow-outs, although there is no evidence that links the origin of these blow-outs to the middens. Studies by Keble (1928), Daley (1931) and Calder (1974) suggest that little damage was done to vegetation by these natives even after inhabiting the areas for 30-40,000 years. Most of the damage/disturbance has been caused by European settlers. Evidence (Report of Senior Land Inspector to the Secretary for Lands, October 1945) suggests that Gunnamatta Beach (at that time known as part of Parish of Fingal) was then used by military forces, and this probably damaged the whole dune system. Even now, in most parts of Gunnamatta, abundant fragments of shrapnel are found in old bomb craters, and plant colonization in some of these sites (e.g. sandy plains) is very slow. More recently, much damage and erosion can be attributed to the large number of visitors and their motor vehicles, including trail bikes and dune buggies, despite attempts by the National Parks Service to protect the dunes (Bird 1975).

Climate

The climatic summary is based on data (1962-80) collected at Cape Schanck situated about 2.5 km south-east of Gunnamatta and corresponds to the Do type of Trewartha (1968): temperate-oceanic-humid with moderate summer and mild winter and adequate rainfall at all seasons. There is little seasonal variation in diurnal temperature range with average daily minimum of 11°C and maximum 17°C. Mean daily temperature maxima vary from 12.2°C in July to 21.9°C in February and mean daily minima from 7.6°C to 14.9°C. Because of a buffering maritime influence, Gunnamatta very rarely experiences prolonged hot weather (above 35°C). Rainfall occurs throughout the year, but there is considerable monthly variation (Fig. 2), the wettest and the driest months being May (84 mm) and January (40 mm), respectively. Nearly 57% of the average rainfall of 741 mm occurs in winter and spring. As with other Victorian

coasts, westerly winds predominate, but with great diurnal variation in direction. Mean monthly wind speed varies from 10-30 km/hour and winds above 40 km/hour occur on 3-8 days per month, the higher frequency being in winter. Relative humidity is moderately high throughout the year (Table 1), but with some seasonal variation. Fog and frost are rare with less than

five fog days per year, and frost recorded only six times in the last nineteen years.

METHODS

Vegetation Analysis

The irregular and complex topography and lack of any chronological sequence with respect to distance from the shore make the choice of method for analysis difficult. From preliminary investigations it appeared that the vegetation pattern could be most easily studied by dividing the whole area into various combined topographic/vegetation units (dune habitat and community combinations) categorised principally (Fig. 3) on the basis of height/depth of topography, exposure and shelter, mobility/stability of the substratum. These units support different vegetation types, each characterized by a particular assemblage of dominant species of high constancy, although associated species may vary greatly. A

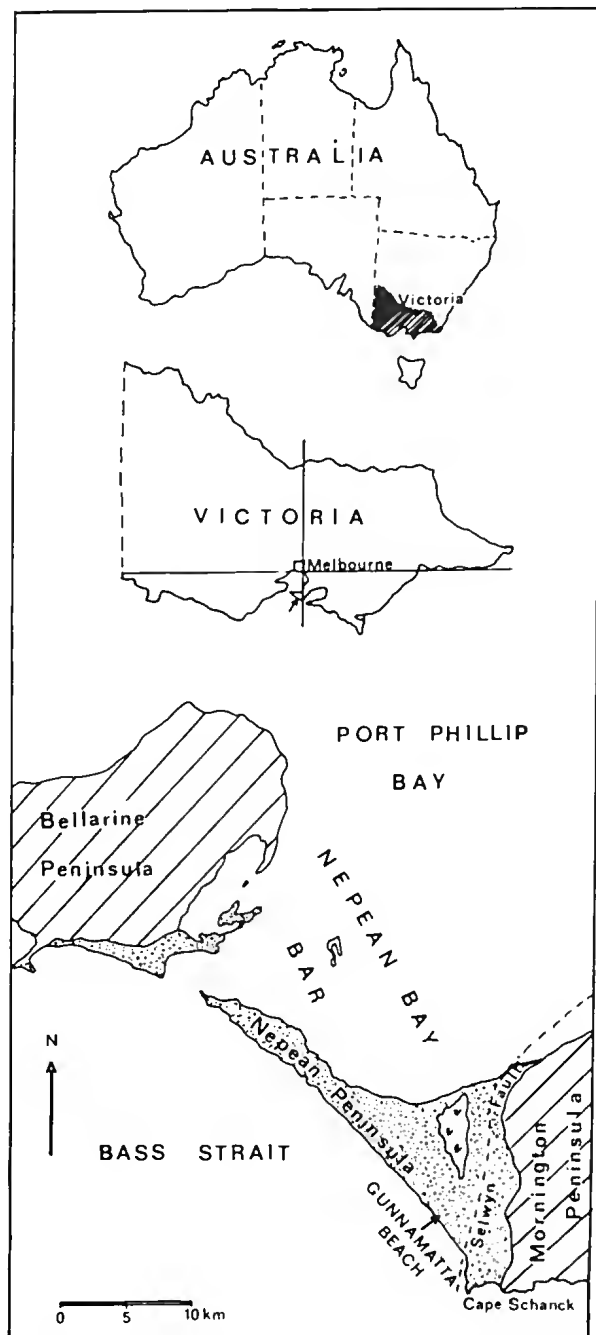


Fig. 1—Location of study area: Gunnamatta Beach, Victoria, Australia. (Simplified map after Bird 1975).

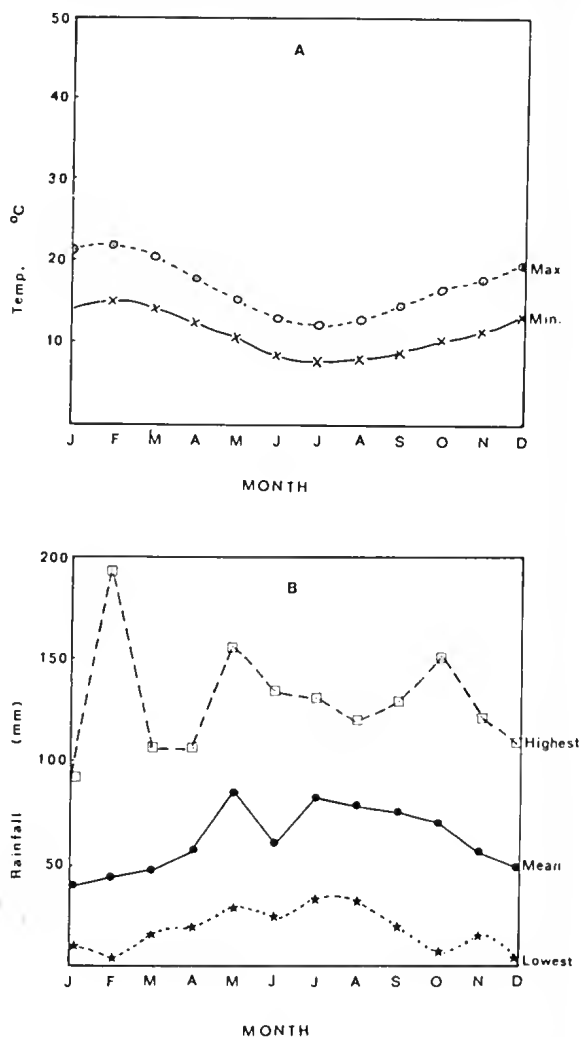


Fig. 2—(A), Average monthly maximum and minimum temperatures. (B), Average monthly, highest and lowest rainfall. (Based on data from Cape Schanck station; 1962-1980).

TABLE 1

SEASONAL VARIATION IN TEMPERATURE, RAINFALL AND RELATIVE HUMIDITY AT GUNNAMATTA (1962-1980)

Season	Temp. (°C)			Rainfall (mm)			R. humidity (%)	
	Max.	Min.	Mean	Max.	Min.	Mean	9 am	3 pm
Summer	21	13.9	17.5	266	52	132	75	70
Autumn	17.9	12.3	15.1	284	94	186	78	71
Winter	12.7	8.0	10.4	318	150	221	84	77
Spring	16.2	10.1	13.1	318	85	202	77	73

natural community nomenclature was thus used (Burnett 1964), which is slightly different from, and more descriptive than, most common dune terminologies. This was considered important in order to cater for the apparent complexity of the dune system without prejudicing its interpretation. To provide an independent check on the correspondence between subjectively determined (topographic) units and vegetation, three random transects were taken from shore to inland [recording cover/abundance in quadrats (50 × 50 cm) on a 4-point scale] crossing many, although not all, topographic units. These quadrats were then subjected to a classification procedure (HISNOB, polythetic divisive using a hierarchical information statistic; Boulton & Wallace 1970, 1973) and Ordination (GOWER ordination on a similarity matrix based on Sørensen's coefficient; Williams 1976). In addition, the vegetation of each unit was recorded at three sites selected for similarity. In each, quadrats (50 × 50 cm) were located by random co-ordinates (Greig-Smith 1964) and frequency, cover and density recorded in both winter (May-June) and summer (November-December) of 1980, recording 1,335 quadrats in all. The vegetation description of a few units was based only on observations. The nomenclature of plant species is based on Willis (1970, 1972).

Soil Analysis

From each topographic/vegetation unit, 5-10 soil samples were collected at 10 cm depth by soil borer. Each sample, consisting of five separate borings thoroughly mixed, was sealed in a polythene bag. Part of each was weighed, oven-dried at 80°C for 24 hours, cooled in a desiccator, re-weighed to give moisture content, then sieved (0.5 mm), and used for analysis: (1) Carbonate content estimated by Collins Calcimeter (Black 1965) and reported as percentage calcium carbonate by weight; (2) Soil pH and conductivity measured on a 1:5 soil water extract, determined by EIL pH meter (7050) with glass electrode, and portable conductivity meter type MC3 (Electronic Instruments, Ltd.); (3) Particle size analysis by sieving (Bagnold 1941); (4) Water-holding capacity (WHC) estimated by the Keen-Razkowski method (Piper 1944, p.82) using small tubes of known diameter and expressed as a percentage of oven dry weight; and, (5) Soil organic carbon content estimated by a slightly modified Walkley and Black method (Piper 1944; Metson 1971).

Salt-Spray Analysis

Relative input of air-borne salt was assessed as by Oosting and Billings (1942) and Boyce (1954). A 5 × 5 cm cut-out in a 15 × 25 cm polythene bag exposed a 6 × 6 cm piece of Kleenex Industrial Tissue fixed by small strips of removable tape. From each tissue four such squares were made, one of which, in an unperforated bag, was used as control. In this way there were four controls for nine salt traps. This was necessary as the indigenous salt content varies appreciably in different tissues. The traps were placed 10 cm above and parallel to the ground and exposed to the wind for five hours. After exposure, the tissues were transferred, using forceps, to numbered glass vials, each shaken in 30 ml of distilled water for one hour and Na⁺, K⁺ and Ca⁺⁺ measured by atomic absorption spectrophotometry (Varian Techtron).

VEGETATION COMPOSITION (See Table 8)

CORRESPONDENCE BETWEEN VEGETATION AND TOPOGRAPHY

Although GOWER has not separated the quadrats into groups as sharply as was considered possible in the field, the vegetation ordination is consistent with subjective classification into topographic units, and HISNOB classification is also consistent with it, although greatly simplified (Fig. 3).

Dunes

These have been considered under three broad categories and further divided into different topographic units, depending upon their origin, situation (distance from sea), mobility/stability of the substratum.

Front dunes: (a) Embryo (b) Initial (c) Old (Formerly Established).

Middle dunes: (a) Mobile (b) Fixed.

Rear dunes.

Front Dunes These, the most seaward line of dunes parallel to the coast, have been further divided into three types:

(a) *Embryo Dunes*: These small 'pre-dunes' or localized depositions of sand, present above High Water Mark but below the initial front dunes, vary in height from 0.5 to 1.5 m and are constantly subjected to erosion by sea and wind and trampling. In spite of this, some species, notably *Cakile maritima* and *Agropyron junceum*, not only survive but are able to form small dunes. The only

TABLE 2
NUMBER OF SAMPLES, RANGE AND MEAN VALUES OF VARIOUS SOIL FACTORS IN WINTER AND SUMMER IN TOPOGRAPHIC UNITS AT GUNNAMATTA. FIGURES IN PARENTHESES INDICATE THE SUMMER VALUES WHILE PRECEDING FIGURES ARE WINTER VALUES.

Topographic Unit	No. of Samples	CaCO ₃ (%)*	pH	O.C.C. (%)	Conductivity (μmhos)	Water Holding Capacity (%)	Dominant Vegetation Type
Front Initial Dunes	15	Mean 22.0 Range 20.0-23.9	8.2 (8.4) 8.1-8.4 (8.3-8.5)	0.135 (0.154) 0.110-0.165 (0.130-0.185)	96 (137) 82-115 (95-155)	21.6 21.1-22.4	<i>Spinifex-Agropyron</i>
Mobile Dunes	15	Mean 24.3 Range 21.9-27.4	8.9 (8.8) 8.8-9.4 (8.7-8.9)	0.159 (0.163) 0.138-0.178 (0.145-0.198)	93 (84) 75-120 (70-100)	22.2 21.8-22.8	<i>Amnophila</i>
Fixed Dunes	20	Mean 21.9 Range 20.6-22.6	8.2 (8.5) 7.9-8.7 (8.1-8.8)	0.298 (0.308) 0.199-0.386 (0.168-0.481)	85 (81) 75-100 (70-100)	24.7 24.5-25.2	<i>Spinifex-Amnophila</i> (old) & Shrubs (annual in summer)
Craters	15	Mean 21.3 Range 20.2-22.6	8.3 (8.5) 8.1-8.6 (8.2-8.7)	0.315 (0.320) 0.195-0.393 (0.199-0.437)	105 (86) 90-125 (70-98)	24.1 23.4-24.6	<i>Spinifex</i> (old) - <i>Scirpus</i> & shrubs (annuals in summer)
Clefts	25	Mean 20.7 Range 18.9-22.0	7.9 (8.0) 7.5-8.3 (7.9-8.6)	0.474 (0.500) 0.364-0.689 (0.313-0.893)	91 (86) 80-100 (75-102)	25.8 25.4-26.0	Shrubs (annuals in summer)
Rear Dunes	10	Mean 19.7 Range 18.4-20.3	7.7 (7.8) 7.4-7.8 (7.7-8.0)	1.93 (1.97) 1.60-2.76 (1.41-2.80)	132 (142) 120-150 (105-175)	32.5 31.5-33.8	<i>Leptospermum</i> closed scrub (annuals in summer)

* Analysis not carried out for summer

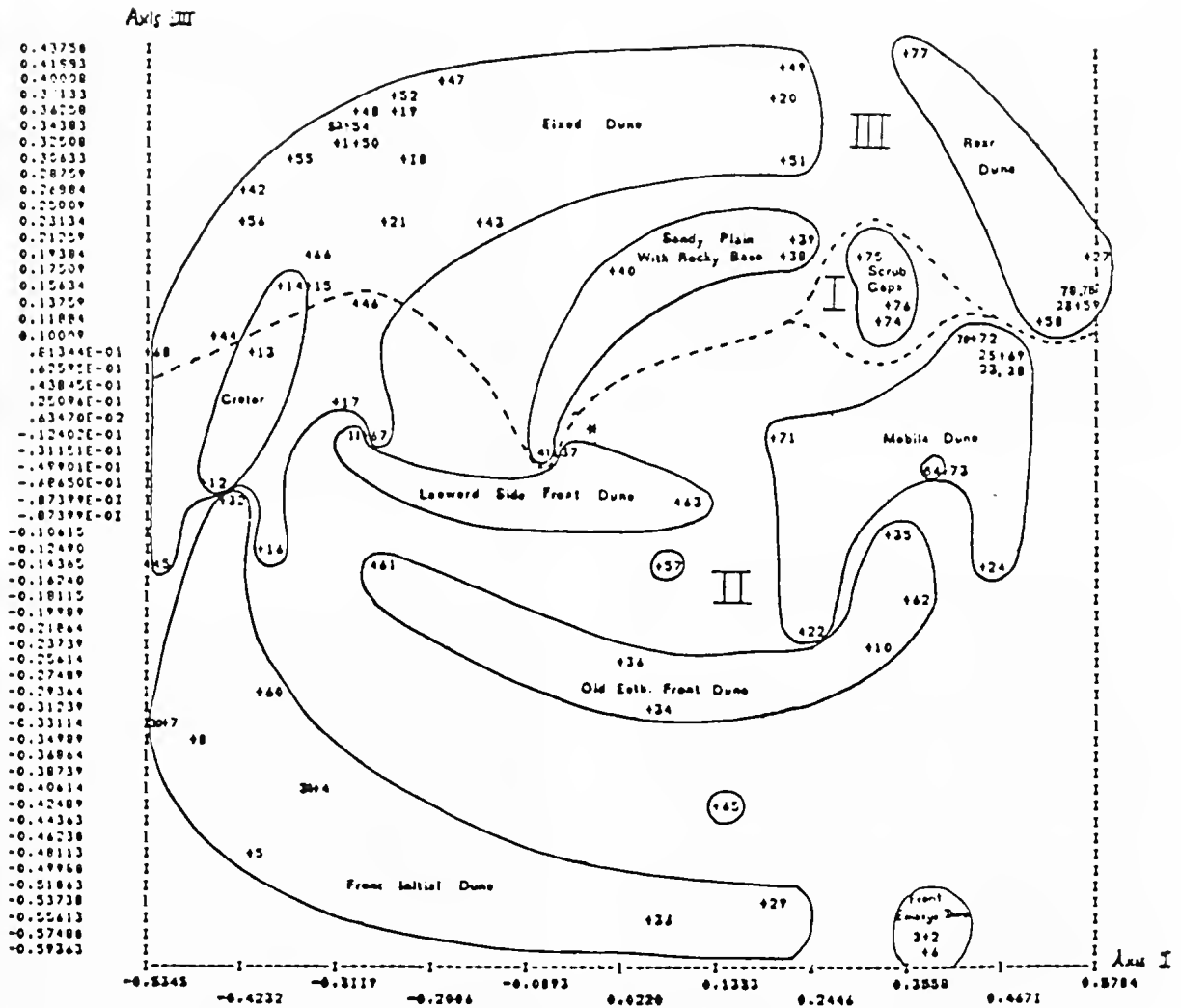


Fig. 3—Scatter diagram of quadrats produced by computer analysis of data of transects using Gower ordination. Group I, II and III produced by HISNOB.

* Represents seven empty quadrats from Sandy Plain.

other species able to survive hereabouts are the grasses *Spinifex hirsutus* and *Ammophila arenaria*, although *Spinifex* seedlings, observed on the beach during summer, did not survive for long and do not appear to contribute to the formation of these dunes.

Embryo dunes have CaCO_3 and organic carbon content values similar to those of initial dunes (Table 2).

(b) *Initial Dunes*: These, the main line of recently-formed front dunes, are flat, 4-20 m wide, of moderate height (1-4 m), generally discontinuous and run parallel to the coast. They are always subjected to wind borne salt, sand, and continual pressure of visitors. Some species, however, gradually build up the dunes and stabilize the substratum, in particular *Spinifex hirsutus* and *Agropyron junceum*, the former being dominant. At Gunnamatta, *Ammophila* either does not occur on initial front dunes or, where present, is found only in localised patches. The two other common species are

Cakile maritima and *Festuca littoralis*. Rarely, a few plants of *Senecio lautus* or *Helichrysum paraliu* (small plants) also occur.

Initial dunes show some variation in soil features, and are characterized by low organic matter in the soil with a high pH and CaCO_3 content (Table 2). The particle size varies from medium to fine grade of sand, with 5% coarse sand.

(c) *Old Established Dunes*: These, the most massive of the front dunes, are 6-10 m high and characterized by generalized erosion, particularly on the seaward sides or blow-outs. In some places, particularly on the eastern end of the Gunnamatta complex, in the absence of embryo and initial front dunes, established dunes form the first line next to the sea and are typically dominated by old woody *Helichrysum paraliu*, with dry, dead branches towards the sea and green sloping branches to leeward. Most noticeable is the complete absence of

Agropyron. Other common plants here include *Spinifex*, *Ammophila*, *Cakile*; occasionally *Senecio laetus*, *Scirpus nodosus* and, in places, *Stackhousia spathulata*, *Calocephalus brownii* and *Melilotus indica* (always under some sort of shelter).

The dune soils are very varied.

(d) *Leeward side of front dunes*: Although not treated here as a separate topographic unit, these stands have tended to segregate out together on Axis III of the ordination (Fig. 3) and constitute a borderline category which would have been worth recognising at a slightly finer resolution. The pattern of vegetation is very diverse, differing every 30–40 m. The plant communities generally dominating are: *Spinifex-Ammophila* or *Helichrysum-Scirpus-Ammophila* or *Spinifex-Festuca-Ammophila*. The other common plants are *Senecio*, *Stackhousia*, *Calocephalus*, *Melilotus* and *Lagurus ovatus* (summer only).

Middle Dunes

One of the most striking topographic units at Gunnamatta, these are characterized by a great variety of dunes—from small to very high (~ 30 m), young and old (although evidence for the real age of such dunes could not be established).

(a) *Mobile Dunes*: This unit most clearly demonstrates the effects of disturbances to formerly established dunes, resulting in complete degradation of vegetation and ensuing erosion. Some such dunes are among the highest at Gunnamatta and are highly mobile and are now dominated by *Ammophila*; exclusively at initial colonization. The consequence of disturbance is clearly seen in the change of pioneer plant species; *Spinifex*, the primary colonizer of initial front dunes, here becomes secondary and establishes itself only after *A. arenaria* has stabilized the substratum to some extent. Despite the mobility, *Festuca littoralis*, common on initial dunes, grows here at only one site. Small numbers occur of *Cakile*, *Senecio* and *Melilotus* although only where sheltered by *Ammophila* plants; as well as a few plants of *Scirpus* and *Stackhousia*, particularly on small dunes 4–5 m in height.

The mobile dunes, always subjected to fresh wind-blown sand, have the highest carbonate content, up to 27.4%, and high pH (Table 2). They have higher organic matter than front initial dunes and moisture content higher than any topographic units, except rear dunes.

(b) *Fixed Dunes*: These differ from the mobile dunes, in topography and vegetation, but most noticeably in the substratum which is almost static except for a slight deposition of wind-blown sand. They are very irregular in outline, commonly cording over the surfaces facing the sea, or by localised blow-outs. The vegetation pattern is compact and diversified. Most of these dunes at Gunnamatta are still dominated by grasses—*Spinifex* and *Ammophila*—although with a marked change in growth form and vigour, here present only as moribund colonies. Although shrubs are abundant they are too scattered at this stage to form a distinct shrubland in their own right. The main shrubs vary from dune to

dune. Those commonly found are: *Acacia longifolia* var. *sophorae*, *Pimelea serpyllifolia*, *Helichrysum paraliu*, *Leucopogon parviflorus*, *Leptospermum laevigatum* and less frequently *Olearia axillaris*. At most places these shrubs are low (2–3 m). The presence of *Melilotus indica* and *Lagurus ovatus* in large numbers (up to 600 plants per m²) during summer is striking. Other plants include: *Senecio laetus*—host of the only parasitic plant, *Orobancha minor*—*Stackhousia spathulata*, *Scirpus nodosus*, *Swainsona lessertiiifolia* and *Carpobrotus aequilaterus*. The appearance of *Clematis microphylla*, *Apium prostratum*, *Acaena anserinifolia* and colonies of mosses can clearly be linked with the amelioration in habitat: increase in organic matter, substrate stability and the shelter afforded by shrubs. In winter, fungi (*Hygrophilus* spp.) and algae (*Nostoc* spp.) are also found. Carbonate content of soil is still very high (21.9%) and pH values show a great variation (7.9–8.7); surprisingly the soils here have the lowest conductivity values (Table 2).

Craters

These are rather flat, bare and exposed in the middle and surrounded by dunes of varying height, thus resembling enclosed amphitheatres. They mostly occur behind the front dunes and between or behind the middle dunes. The substratum is relatively stable, the loose sand having been removed by explosions frequently exposing a former, harder soil surface; but some craters are situated near the shore and hence receive substantial amounts of salt-spray and fresh-blown sand. Although much more sheltered than fixed dunes, craters are less diversified in vegetation, dominated by a *Spinifex* (old plants)—*Scirpus* community, *Ammophila* being present only in patches. The shrubs (1–2 m tall) commonly found here are—*Helichrysum*, *Leucopogon*, *Calocephalus* and occasionally *Acacia*, *Pimelea* and *Olearia*. Of the annuals, *Melilotus* is more frequent than *Lagurus* during summer. Perennials include: *Senecio*, *Stackhousia*, *Carpobrotus* and occasionally *Swainsona*. Mosses also occur, especially under the shrubs.

There is little difference in soil characters compared with fixed dunes, most notably a higher conductivity; a slight increase in organic matter content (Table 2) and moisture content, may not be significant.

Clefts

These are narrow sheltered areas which lie mainly between the middle dunes, mobile or fixed, and in places demonstrate the vegetation pattern prior to disturbances. Most appear to have been formed as a result of the building up of dunes around them, rather than by excavation. Being sheltered, they generally receive negligible wind-blown salt-spray and sand. The diversity in vegetation, and the presence of even mesophytic species in some clefts, clearly indicate significant differences in habitat conditions from other parts of Gunnamatta. The plant species show an inter-mixture of original and recent vegetation and include some species not found elsewhere. The vegetation at most places is dominated by shrubs such as *Leptospermum laevigatum*

(mostly old plants), *Acacia longifolia* var. *sophorae*, *Leucopogon parviflorus*, *Pimelea serpyllifolia* and *Olearia axillaris*. The *Spinifex*–*Ammophila* community is present, mostly as reliets, with a greatly reduced cover, whereas *Scirpus nodosus* is more frequent, although it covers less area, and *Carpobrotus aequilateris* is common. Other plant species regularly found, though scattered, are: *Swainsona lessertiiifolia*, *Stackhousia spathulata*, *Senecio lartus*, *Orobanche minor*, *Sonchus megalocarpus* and—in some of the clefts—*Dichondra* spp., *Apium prostratum*, *Acaena anserinifolia*, *Kennedia prostrata*, very restricted at Gunnamatta, is found in some clefts. In summer, *Lagurus ovatus* is the most frequent and abundant annual with *Melilotus indica* not quite so plentiful. Mosses here cover a much greater ground area, again indicating different habitat conditions.

A slight decrease in carbonate and pH with an increase in organic matter and moisture content (4.1%) is observed, but the soil is still very rich in CaCO_3 and is still alkaline (Table 2).

Rear Dunes

This unit, which supports the present-day final stabilized community, is dominated by *Leptospermum* closed-serub which, prior to disturbance, apparently extended to near the sea as indicated by the presence of isolated old individuals throughout Gunnamatta, particularly on the eastern side, close to the shore. The closed-serub, in general, lacks any understorey vegetation, except in areas where light is not the limiting factor. Two old trees of *Banksia integrifolia* in one locality, perhaps point to the possibility of a formerly more complex woodland. Epiphytic lichens and the liverworts *Frullania* spp. and *Austrolejeunea nudipes* (Hook. f. and Tayl.) Grolle, indicate a surprisingly humid microclimate within this community type.

A decline in CaCO_3 content, pH and increase in organic matter is observed, but the soil still does not show any profile differentiation (Table 2).

Blow-Outs

The formation of this topographic unit, a common feature of Gunnamatta, is clearly associated with past disturbances. Although it is impossible to determine the origins of the disturbances, the evidence suggests that natural and man-made activities (trampling, vehicles, military and perhaps aboriginal activities) are likely to be responsible for the degradation of the vegetation and, consequently, initiation of blow-outs. Some blow-outs are extensive, up to 150×70 m. The leeward sides develop into parabolic dunes, of which some are large and mobile, the great mobility apparently hindering colonization. Although conditions for growth are very stringent, some species, mainly *Ammophila*, *Spinifex* and *Cakile*, are able to survive, and in places on the leeward side, *Spinifex* and *Ammophila* grow very luxuriantly. Surprisingly, some blow-outs are among the very few sites where seedlings of both *Ammophila* and *Spinifex* have been observed during summer. Very rarely, young plants of *Helichrysum* occur.

In soil characteristics, the blow-outs are very similar to mobile dunes.

Sandy Plains

These are flat and exposed, like craters, but covering a very large area, and can be situated either close to the shore or adjacent to the inland vegetation. Their formation is further evidence of disturbance by military activities; where, even after more than 40 years, fragments of bullets and shrapnel can be found on the surface. The plains are either devoid of any vegetation or, in some places, *Ammophila* and *Spinifex* occur round the edges slowly advancing towards the centre. Colonization appears to be very slow because of limited supply of fresh sand and, at present rates, it will take decades, if not centuries, before these areas are colonized completely.

Seedlings of *Spinifex*, *Ammophila* and *Melilotus* have been observed but none survived.

Miscellaneous Units

(a) *Sandy Plain with Rocky Base*: This topographic unit, found at only one place in Gunnamatta between a front and middle dune, is common on adjacent coasts. It is characterized by the presence of rhizoconerations and limestone rock beneath a thin covering (30 cm) of bare sand. The vegetation is typically very uniform, open, and dominated by a *Calocephalus-Scirpus* community. *Ammophila* is totally absent, and *Spinifex* is present only in small patches. *Stackhousia* is the most frequent annual. Other commonly occurring plants are *Carpobrotus*, *Senecio* and, during summer, *Melilotus*. Small shrubs of *Helichrysum paraliun* are also present, but are very scattered.

(b) *Dune Hollows Rich in Organic Matter*: These are small hollows, more or less surrounded by old *Leptospermum* shrubs. The substratum is relatively rich in organic matter, and receives almost no supply of wind-blown sand or salt-spray. The most abundant plant is *Swainsona*, particularly near the margins of *Leptospermum* patches. *Carpobrotus* and *Senecio* are the most frequent perennials and during summer *Melilotus* and *Lagurus* occur in large numbers. Both *Ammophila* and *Spinifex* are present, but only as reliets. Mosses cover a substantial proportion (>45%) of the ground area.

(c) *Scrub-gaps*: These are small gaps formed as a result of some sort of disturbance, especially to the aerial parts of *Leptospermum* closed-serub, leaving behind old woody stems. The substratum is fully stabilized because of relatively high amounts of organic matter in the soil, but being exposed they receive some blown sand. This topographic unit demonstrates a completely different vegetation pattern, the distinctive feature being the presence of mosses such as *Barbula torquata* and *Tortella calycina* covering almost 70% of the ground area. Other noticeable features are the presence of *Swainsona*, *Senecio* and *Leucopogon* as the most common plants, and the complete absence of all pioneer species. Other species found here are—*Pimelea serpyllifolia*, *Stackhousia spathulata*, *Scirpus nodosus*, *Carpobrotus aequilateris*, *Melilotus indica* and *Lagurus ovatus* (in summer).

PATTERN IN TIME AND SPACE

The complexity and irregularity in topography, further aggravated by the lack of any fixed relationship of topographic units with distance from the sea, are clearly evident in the vegetation pattern which seems, at first glance, to exemplify anarchy rather than causality. There is no obvious logical pattern in topography and vegetation, but rather a mosaic of vegetation which is complex and apparently irrational. Plant communities growing immediately adjacent to each other may belong to pioneer and final (stabilized) stages, a vegetational paradox typical of Gunnamatta. Nor do the shrub communities demonstrate any consistent pattern and different species combinations are found at different sites even of the same topographic unit. This floristic diversity within an apparently homogeneous habitat is unpredictable and presumably reflects different origins, ages (time since stabilization), and habitat development. An ecologically significant feature is the change in vegetation pattern, resulting from disturbances. For example, on mobilised middle dunes *Ammophila* becomes the first colonizer instead of *Spinifex*. Similarly in scrub-gaps, *Swainsona*, *Senecio* and *Leucopogon* are the first colonizers; normally these plants appear during the second phase of succession.

From the soil analysis (Table 2) it is apparent that soil at Gunnamatta is calcareous and still alkaline in all topographic units. There is slight decrease in the amount of calcium carbonate, from 24.3% (mobile dune) to 19.7% in the rear dunes, perhaps because of initial high CaCO_3 and incomplete leaching. In this respect Gunnamatta shows a similarity to the highly calcareous dunes of the Outer Hebrides (Gimingham 1951). Although the soil is still alkaline even in older topographic units (rear dunes) it shows a pattern of general decrease with age (stabilization). There is, however, no constant relationship of pH decrease with increase in distance from sea. As

in other dune systems (Salisbury 1922, 1925, Gimingham 1951), the sands are initially poor in organic matter but this increases significantly in the later stages of succession. Soil salinity is negligible in most of the topographic units, because most of the salts are washed away by rain.

Relationship of topographic units and soil factors

Of the several factors investigated— CaCO_3 , pH, organic carbon content, conductivity, moisture content, soil particle size—only soil organic carbon content shows any kind of consistent relationship with different vegetation types. Water Holding Capacity is closely related to organic carbon content, as would be expected. In topographic units where soil organic carbon content is low (<0.17%), vegetation mainly consists of pioneer plant species (*Cakile*, *Spinifex*, *Agropyron*, *Ammophila*) (Table 2); but, where the soil organic carbon content exceeds c 2% it is mainly dominated by *Lepidospermum* closed-scrub. With intermediate values of soil organic carbon content, the vegetation varies.

Species Distribution at Gunnamatta

The complex vegetation pattern at Gunnamatta has no apparent overall consistency, but some species (e.g. *Melilotus indica*, *Senecio lantus*) are widely distributed while some others (e.g. *Agropyron junceum*, *Cakile maritima*) are restricted. An attempt was therefore made to determine whether there were habitat factors controlling, limiting or at least correlated with the distribution of individual species, rather than vegetation. Several probable factors (Table 3), some of which have been shown to be the major controlling/limiting factors in other dune systems [salt-spray (Oosting & Billings 1942, Martin 1959, Parsons & Gill 1968, Randall 1974, Barbour 1978); pH (Burgess & Drover 1953, Böcher 1954)], were considered in some detail. Other factors, such as precipitation, air temperature, light and wind, were felt to affect the overall vegetation, generally

TABLE 3
VARIOUS HABITAT FACTORS CONSIDERED IN DIFFERENT AREAS FOR VEGETATION ZONATION / SPECIES DISTRIBUTION

Factors	Area	Authors and Year
Wind	East Mediterranean Coasts, Israel	Zohary & Fahn (1952)
Salt-spray	Bogue Bank, N. Carolina, U.S.A.	Oosting & Billings (1942)
	East Mediterranean Coasts, Israel	Zohary & Fahn (1952)
	Island Beach State Park, U.S.A.	Martin (1959)
	Wilson's Promontory, Victoria, Australia	Parsons & Gill (1968)
	Monaeh Isles National Nature Reserve, Outer Hebrides	Randall (1974)
Sandmovement/ substrate stability	Coastal sandy shores, Japan	Nobuhara (1967)
	Cape Haiteras National Seashore, U.S.A.	Van der Valk (1973)
	Donana National Park, Spain	Garcia Nova (1979)
Moisture content	Eastern Cape Coast, South Africa	Lubke & Avis (1982)
Water-table	Braunton Burrows, U.K.	Willis <i>et al.</i> (1959)
Particle-size	Greek Coasts, Greece	Lavrentiades (1975)
Soil salinity	Barbados Coast, Barbados	Gooding (1947)
pH	European coasts, Europe	Böcher (1954)

TABLE 4

pH RANGES OF MAIN SPECIES AT GUNNAMATTA (RESULTS BASED ON 30-60 SAMPLES FOR EACH SPECIES)

Species	pH range
<i>Acacia longifolia</i> var. <i>sophorae</i>	7.9-8.7
<i>Agropyron junceum</i>	7.6-9.1
<i>Amnophila arenaria</i>	8.0-9.4
<i>Cakile maritima</i>	7.5-9.0
<i>Calocephalus brownii</i>	7.5-9.1
<i>Carpobrotus aequilaterus</i>	7.6-8.9
<i>Festuca littoralis</i>	8.0-8.8
<i>Helichrysum paraliium</i>	7.8-8.6
<i>Kennedia prostrata</i>	7.4-8.9
<i>Lagurus ovatus</i>	7.6-8.5
<i>Leptospermum laevigatum</i>	7.4-8.6
<i>Leucopogon parviflorus</i>	7.4-8.4
<i>Melilotus indica</i>	7.6-9.0
<i>Olearia axillaris</i>	7.6-8.9
<i>Pimelea serpyllifolia</i>	7.7-8.5
<i>Scirpus nodosus</i>	7.5-8.9
<i>Senecio lautus</i>	7.5-8.8
<i>Spinifex hirsutus</i>	7.7-9.1
<i>Stackhousia spathulata</i>	7.7-9.2
<i>Swainsona lessertiiifolia</i>	7.5-9.0

without a significant local effect. The factors—particle size, moisture content, sand movement and soil salinity—were not found to be major factors limiting the occurrence of species to particular dune habitats although, on a much smaller scale, they may influence the distribution of individual plants, especially during the germination/early establishment phase. Soil pH

(Table 4) was also found to have no correlation with the occurrence of particular species. Salt-spray, considered to be a major causal factor of vegetation zonation/species distribution in different parts of the world by various workers (Table 3), was also investigated in detail, but results (Table 5) showed that no gradient in salt deposition was observed at Gunnamatta, and no vegetation pattern corresponded to the pattern of deposition of salt. Salt-spray, therefore, cannot be considered a major or decisive factor influencing the spatial distribution of plant species, although it has been observed to influence some species by killing seedlings during sudden blasts of salt-spray or by damaging the shoot apex/leaves of some plants especially on front dunes. The pattern of influence, however, is neither predictable nor, *a posteriori*, discoverable.

The correlation observed between vegetation and soil organic carbon content (O.C.C.) may be interpreted as evidence of either a cause or an effect of the presence of particular species. Since O.C.C. was the only factor which showed any kind of direct relationship with different vegetation types, the hypothesis was made that O.C.C. could be a factor correlated with, or even determining, species establishment at particular sites. This was first investigated with *Cakile maritima* and then extended to 18 other species (Sacheti 1981). Each species is associated with a particular O.C.C. range, sometimes rather narrow (Table 6). Species with narrow ranges (<20% of the total range) are generally confined to localities with low O.C.C., and have a restricted distribution; species with medium, wide and full ranges have a moderate to wide distribution. Species with narrow ranges are pioneers and early colonizers of dune

TABLE 5
DISTRIBUTION OF CATIONS AT TWELVE DIFFERENT SITES (ppm/cm²)

Wind Direction Site No.	Na ⁺	SE Ca ⁺⁺	K ⁺	Na ⁺	SW Ca ⁺⁺	K ⁺	Na ⁺	NE Ca ⁺⁺	K ⁺	Na ⁺	NW Ca ⁺⁺	K ⁺
1.	0.041	0.031	0.002	0.095	0.030	0.004	0.072	0.024	0.006	+	+	+
2.	0.115	0.031	0.002	0.071	0.025	0.003	0.045	0.038	0.008	0.050	0.012	0.004
3.	0.125	0.055	0.005	0.071	0.033	0.003	0.037	0.024	0.008	0.060	0.019	0.021
4.	0.050	0.024	0.001	0.011	0.028	0.004	0.029	0.020	0.010	0.056	0.018	0.018
5.	0.036	0.017	0.001	0.053	0.034	0.004	0.041	0.020	0.009	0.022	0.009	0.005
6.	0.066	0.031	0.001	+	+	+	0.029	0.020	0.001	0.033	0.016	0.008
7.	0.043	0.022	0.001	0.180	0.031	0.004	0.039	0.015	0.016	0.045	0.015	0.012
8.	0.080	0.019	0.001	0.074	0.032	0.002	0.072	0.018	0.004	0.050	0.012	0.007
9.	0.087	0.029	0.001	0.217	0.039	0.008	0.128	0.086	0.006	0.062	0.019	0.012
10.	0.520	0.066	0.017	0.560	0.056	0.042	0.080	0.031	0.006	0.059	0.019	0.014
11.	0.087	0.024	0.001	0.463	0.061	0.045	0.119	0.024	0.051	0.048	0.022	0.019
12.	0.235	0.045	0.008	0.801	0.102	0.050	0.148	0.031	0.050	0.065	0.027	0.031

Brief description of the sites

- | | |
|---|--|
| 1. = High Mobile Dune (near inland) | 2. = Sandy plain (near inland vegetation) |
| 3. = Eroding Dune (behind middle dune) | 4. = Fixed dune (high; middle of Gunnamatta) |
| 5. = Partly exposed crater (middle of Gunnamatta) | 6. = Small sheltered dune hollow |
| 7. = Small fixed dune (facing south) | 8. = Cleft (surrounded by dunes) |
| 9. = Open, exposed sandy plain (behind front dunes) | 10. = Eroding face of dune (near sea) |
| 11. = Leeward side of blow-out (near sea) | 12. = Front Initial Dune |

+ Salt-traps removed by visitors

TABLE 6
O.C.C. RANGES OF MAIN SPECIES AT GUNNAMATTA

Species	O.C.C. Range (%)	Proportion of
		Total range (%)
<i>Agropyron junceum</i>	0.10-0.17	2.7
<i>Spinifex hirsutus</i>		
(young plants)	0.11-0.25	5.2
(old plants)	0.25-0.75	18.5
<i>Ammophila arenaria</i>		
(young plants)	0.10-0.26	5.9
(old plants)	0.26-0.97	26.3
<i>Cakile maritima</i>	0.10-0.28	6.7
<i>Festuca littoralis</i>	0.10-0.33	8.4
<i>Stachys spathulata</i>	0.12-0.60	17.4
<i>Calceophalus brownii</i>	0.11-0.62	18.6
<i>Acacia longifolia</i> var. <i>sophorae</i>	0.20-0.72	21.5
<i>Helichrysum paraliuum</i>	0.15-0.84	25.5
<i>Kennedia prostrata</i>	0.23-0.99	27.8
<i>Olearia axillaris</i>	0.22-0.99	28.6
<i>Carpobrotus aequilaterus</i>	0.15-0.99	30.7
<i>Scirpus nodosus</i>	0.16-1.09	34.4
<i>Lagurus ovatus</i>	0.19-1.46	47.0
<i>Melilotus indica</i>	0.15-1.43	47.4
<i>Senecio laevis</i>	0.14-1.51	50.7
<i>Swainsona lessertiiifolia</i>	0.15-1.55	51.8
<i>Pinelia serpyllifolia</i>	0.23-1.66	52.8
<i>Leucopogon parviflorus</i>	0.20-2.68	91.5
<i>Leptospermum laevigatum</i>	0.22-2.80	95.4

succession, species confined to medium and wide ranges appear during the second stage of succession, and those corresponding to full range are co-dominants and dominants of the final stabilized stage (Table 7). Thus it appears that if O.C.C. is limiting (directly or indirectly), species with narrow ranges are the ones whose occurrence is most likely to be limited by the amount of organic carbon in the soil, whereas the distributions of species belonging to medium and higher ranges are likely to depend on several other factors as well, e.g. intolerance to burial and salinity (Sacheti 1983), substratum stability, soil temperature etc. The significance of O.C.C. ranges will be discussed in detail in a separate paper.

Seasonal Variation

Results of the vegetation analysis replicated in winter (May-June) and summer (Nov.-Dec.) suggest that there is little seasonal variation in the vegetation pattern—the only significant difference is in the presence, in summer, of the annuals *Melilotus* and *Lagurus* in large numbers in some of the topographic units, for example, fixed dunes, clefts, craters. Extensive data over at least 3-4 years would be required to detect and confirm significant changes taking place in perennial species. As would be expected, soil characteristics showed no detectable change (Table 2) in most factors investigated, although a slight increase in organic carbon content and pH was observed. Moisture content was the only factor which

showed a difference in winter and summer values and that is a transient feature.

Succession

The results of two kinds of successional change (primary and secondary) can be observed at Gunnamatta, although the changes in vegetation with time can only be deduced from the patterns existing at present (Scott 1965). Aerial photographs do not span a great enough time, nor are they sufficiently detailed, to reveal what has actually happened. The conversion of bare sand, freshly provided by the sea, into woodland, is primary succession, and the re-working of rejuvenated older sediments, leading towards a similar result is considered to be secondary succession. The forces driving primary succession are autogenic, changes induced by the plants themselves modifying the habitat, whereas secondary succession, although similar in principle, is triggered by erosion. If the erosion is repeated, the succession may be more or less cyclical. "Disturbance creates patches of successional environments whose size depends on the type and severity of the disturbance" (Pickett 1976).

Disturbance has played a crucial role in the development of Gunnamatta into a complex dune system; hence it is almost impossible to locate even a small area which shows a series of successional stages in spatial and chronological order. Without dune ages, no rigid correspondence could be established between the age of the dunes and phases of succession. Thus succession can only be deduced by arranging the various stages of vegetation development in a logical sequence from areas of initial colonization of bare sand to the present-day final stage. The pattern deduced is subjective, but plausible, and corresponds to Connell and Slatyer's (1977) facilitation model 1. Since, undoubtedly, disturbances have played an important role in the make-up of this area, it would be logical to consider the succession under two headings (see Fig. 4): 1. Undisturbed succession (Primary); and, 2. Disturbed succession (Secondary).

Undisturbed succession

In the absence of any major disturbance, this can still be observed in the far eastern part of Gunnamatta. It is similar to other Victorian dune systems although the dominant plant species are different. The important stages are:

(a) *Grassland stage*: This starts on front embryo/initial dunes with the colonization of bare, mobile sand, low in organic matter, by plant species such as *Cakile maritima*, *Spinifex hirsutus* and *Agropyron junceum*. By sand accumulation and continued survival in harsh conditions (e.g. windblown sand, salt-spray, mobile substratum, trampling) these plants gradually stabilize the sand enabling other species to become established. Other taxa, such as *Ammophila arenaria* and *Festuca littoralis*, arrive later and become important contributors to ameliorating edaphic conditions by increasing organic matter content (and, hence, water holding capacity) and stability. Eventually, however, the changed habitat conditions appear to become less suitable for the existence

TABLE 7

DISTRIBUTION OF VARIOUS SPECIES AT GUNNAMATTA

FED=Front embryo dunes; FID=Front initial dunes; OFD=Old established front dunes;
 LFD=Leeward side of front dunes; MD=Mobile dunes; FxD=Fixed dunes; RD=Rear dunes;
 Cr=Craters; Cl=Clefts; SG=Scrub gaps; DH=Organic matter rich dune hollows; BO=Blow outs;
 SP=Sandy plains; SPRB=Sandy plains with rocky base.

Species	O.C.C. Range	Distribution at Gunnamatta
<i>Agropyron junceum</i>		FED, FID
<i>Spinifex hirsutus</i> (young plants)		FID, LFD, SP, MD, BO
(old plants)		FxD, Cr, Cl, DH
<i>Amnophila arenaria</i> (young plants)	NARROW RANGE	MD, FID, LFD, SP, BO
(old plants)		FxD, Cr, Cl, DH
<i>Cakile maritima</i>		FED, FID, LFD, MD, SP, BO, OFD
<i>Festuca littoralis</i>		FID, LFD, Cr, MD, OFD
<i>Stackhousia spathulata</i>		SP, FxD, Cr, Cl, SPRB, LFD, DH
<i>Calocephalus brownii</i>		
<i>Acacia longifolia</i> var. <i>sophorae</i>		SPRB, SP, Cr, LFD
<i>Helichrysum paraliun</i>		FxD, Cr, Cl, LFD, DH
<i>Olearia axillaris</i>	MEDIUM RANGE	OFD, FxD, Cr, Cl, SPRB, SG
<i>Carpobrotus aequilaterus</i>		FxD, Cr, Cl, SG, DH, LFD
<i>Scirpus nodosus</i>		FxD, Cr, Cl, DH, LFD, SPRB
<i>Lagurus ovatus</i>		Cr, FxD, Cl, SPRB, SG, DH, LFD
<i>Melilotus indica</i>		Cl, FxD, SG, DH, Cr, RD, LFD, SP, SPRB
		FxD, Cl, Cr, DH, SG, RD, LFD, SP, OFD, SPRB, OFD, FED, MD
<i>Senecio lautus</i>	WIDE RANGE	FxD, Cl, Cr, SG, DH, RD, LFD, OFD, SP, SPRB, FED, MD
<i>Swainsona lessertiiifolia</i>		FxD, Cl, Cr, SG, DH, RD, LFD, OFD, SP
<i>Pimelea serpyllifolia</i>		FxD, Cl, Cr, RD, SG, DH, LFD
<i>Leucopogon parviflorus</i>	FULL RANGE	RD, Cl, FxD, Cr, DH, SG, LFD, OFD
<i>Leptospermum laevigatum</i>		RD, Cl, FxD, Cr, DH, SG

of these pioneers/early colonizers and the sites are then invaded by other plant species.

(b) *Old grassland/shrub community stage*: This is marked by a change in vegetation structure from being open, sparse and uniform to compact and diversified. The changes in habitat (reduced supply of fresh-blown sand, increase in organic matter content, competition with other plants) result in, or are accompanied by, the gradual decline, especially of grasses—*Spinifex hirsutus* and *Amnophila arenaria*—and the appearance of shrubs and annuals. At most sites this stage is still dominated by an old grass community of *Spinifex* and *Amnophila*, but is also marked by the presence of shrubs, mosses, and large numbers of *Melilotus* and *Lagurus* during summer. This second stage of succession, certainly the most diversified of all, would gradually lead to domination by shrubs and the decline and ultimate loss of most herbaceous species.

(c) *Closed-scrub stage*: The gradual decline of most grasses, herbaceous perennials, and annuals, and the corresponding rise to dominance of shrubs, bring about the final stage. Initially dominated by a variety of taller shrubs, later it comes to consist of *Leucopogon*-

Leptospermum community and finally (as far as present vegetation goes) *Leptospermum* closed scrub.

Disturbed Succession

Except for the eastern end of Gunnamatta, the original vegetation dominated by *Leptospermum* closed-scrub has mostly been damaged (partially or totally), and the complete primary succession is scarcely evident. But this disturbance has resulted in opening new sites for secondary succession, most of which are similar to those associated with primary succession, in that colonization starts from bare sand, generally low in organic carbon (~0.15%), although in some sites, e.g. scrub-gaps, the substratum is relatively rich in organic matter (~0.44%). Secondary succession differs from primary mainly in the unpredictable course it follows. Probably in some sites it is similar to primary succession, but may never reach any stabilized stage or else the pattern may be altogether different. Whatever its direction, the pattern of secondary succession is likely to be of significance as an indicator for future management.

The main topographic units from which the secondary succession appears to have started are: (i) Re-

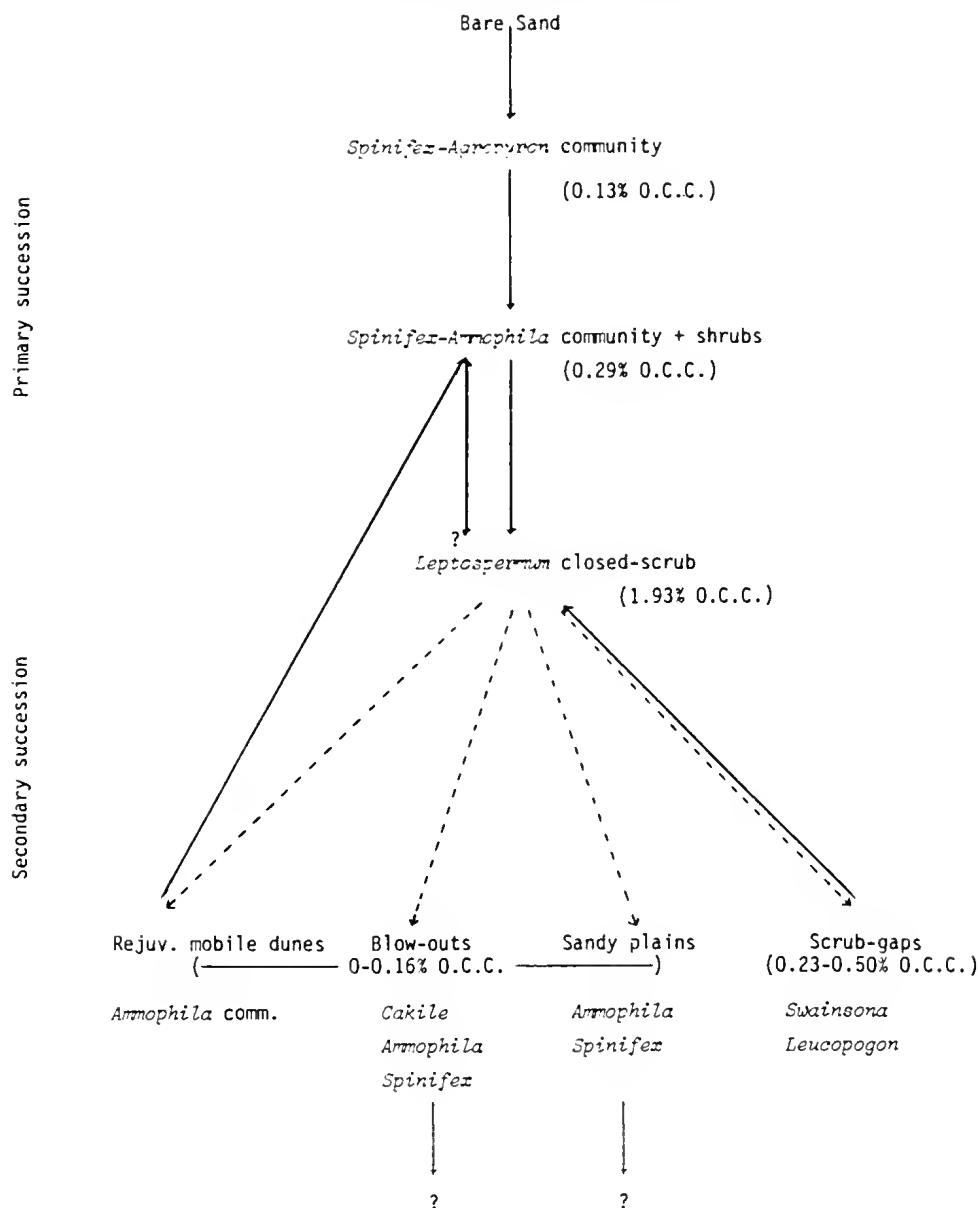


Fig. 4—Summary of types, pattern and direction of succession at Gunnamatta.

juvenated mobile dunes; (ii) Blow-outs; (iii) Sandy plains; and, (iv) Scrub-gaps. Of these, the first three have somewhat similar conditions in that the substratum is mobile (moderate to heavy deposition/erosion of sand), bare and low in organic matter. In all three, a change in pioneer colonizing species is observed; for example in mobile dunes, *Ammophila* has replaced *Spinifex*; in blow-outs and sandy plains the process of colonization appears to be extremely slow and in most places there is an assemblage of *Spinifex-Ammophila-Cakile* as pioneer plants.

As the first three units at Gunnamatta, especially (ii) and (iii), are still in the initial stages of colonization it

would not be reasonable to predict the direction in which they will proceed, because this would, in all probability, be determined by several factors. The outstanding difference between these (i-iii) and scrub-gaps (iv) is in the type of colonizers. Scrub-gaps are singular in that early colonizers here are *Swainsona*, *Senecio* and *Leucopogon* rather than *Spinifex*, *Ammophila* and *Cakile*—not only in the early stages of primary succession but also in secondary succession. It seems likely that the principal factor to which this difference may be attributable is the type of substratum, which is relatively rich in organic matter and has greater stability. Like other sites of secondary succession at Gunnamatta,

TABLE 8
THE MEANS OF PERCENTAGE FREQUENCY (F) AND COVER (C) OF DIFFERENT SPECIES IN MAIN TOPOGRAPHIC UNITS AT GUNNAMATTA. MEANS ARE BASED ON DATA OF THREE SITES FOR ANY TOPOGRAPHIC UNIT.

	Front Initial Dune		Mobile Dune		Fixed Dune		Crater		Cleft	
	F	C	F	C	F	C	F	C	F	C
<i>Acacia longifolia</i> var. <i>sophorae</i>	—	—	—	—	3	+	—	—	11	4
<i>Agropyron junceum</i>	96	7	—	—	—	—	—	—	—	—
<i>Ammophila arenaria</i>										
(young plants)	19	2	51	13	—	—	—	—	—	—
(old plants)	—	—	—	—	52	9	7	2	25	3
<i>Ancaena anserinifolia</i>	—	—	—	—	2	+	—	—	2	+
<i>Apium prostratum</i>	—	—	—	—	3	+	—	—	—	—
<i>Cakile maritima</i>	6	1	2	+	—	—	—	—	—	—
<i>Calocephalus brownii</i>	—	—	—	—	—	—	14	5	5	+
<i>Carpobrotus aequilaterus</i>	—	—	—	—	17	2	10	1	28	4
<i>Clematis microphylla</i>	—	—	—	—	9	1	—	—	10	+
<i>Crassula sieberana</i>	—	—	—	—	8	+	5	+	2	+
<i>Festuca littoralis</i>	6	1	—	—	—	—	5	+	—	—
<i>Helichrysum paraliun</i>	3	1	—	—	10	2	17	3	18	7
<i>Kennedia prostrata</i>	—	—	—	—	—	—	—	—	3	+
<i>Lagurus ovatus</i>	—	—	—	—	57	3	20	1	69	4
<i>Leptospermum laevigatum</i>	—	—	—	—	10	2	2	1	11	8
<i>Leucopogon parviflorus</i>	—	—	—	—	24	4	8	3	33	7
<i>Melilotus indica</i>	—	—	—	—	59	5	67	4	60	5
<i>Olearia axillaris</i>	—	—	—	—	5	1	4	1	6	1
<i>Orobanche minor</i>	—	—	—	—	3	+	2	+	4	+
<i>Pimelea serpyllifolia</i>	—	—	—	—	16	2	7	1	29	4
<i>Scirpus nodosus</i>	—	—	—	—	18	3	34	4	42	4
<i>Senecio laetuis</i>	3	+	—	—	33	2	23	1	28	2
<i>Spinifex hirsutus</i>										
(young plants)	84	14	6	1	—	—	—	—	—	—
(old plants)	—	—	—	—	50	10	42	7	23	3
<i>Stackhousia spathulata</i>	25	+	—	—	18	+	12	1	3	+
<i>Swainsona lessertifolia</i>	—	—	—	—	3	+	5	+	7	+

+ indicates less than 1% cover

— indicates absence of a species

scrub-gaps are at present only in a very early stage of colonization so that the future trend of succession is unclear. But since the habitat conditions and plant species here are comparable to the second stage of primary succession, it may be conjectured that primary and secondary succession will converge at this point. The pattern of primary succession at Gunnamatta is somewhat similar to that of other dune systems in Victoria (Turner, Carr & Bird 1962, Barson & Calder 1981) although the dominant species are different. More studies are required to assess the effects of disturbances in modifying the pattern of primary succession.

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REGENERATION OF *HETERODENDRUM* IN ARID SOUTH-EASTERN AUSTRALIA

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ABSTRACT: Work was carried out to see if the failure of *Heterodendrum oleifolium* to regenerate vegetatively and from seed in the arid zone is due to grazing, the physical environment, innate factors or some combination of these. Flowering and seed set were spasmodic in the study area. Insect predators destroyed up to 68 per cent of seed in the crowns. Many unattacked seeds were empty and the proportion of empty seeds appeared to increase with time from seed set. Enhanced germination after seed coat nicking demonstrated some hard-seededness.

Sucker shoots can arise from shallow, horizontal roots. Detached root pieces produced callus tissue but not suckers. Young plants readily produced stem suckers after decapitation. After root severance, callus swellings were common, but root suckering was rare. In the field, severance of roots by ploughing produced root suckers distal to the site of severance, suggesting control of suckering by the shoot apex. After wildfire, 19 per cent of mature trees were killed, mostly those smaller than 50 cm girth, while 30 per cent formed root suckers. At all sites, virtually all root suckering could be readily related to specific disturbance events and so was considered episodic.

Isoenzyme analysis to test genetic identity indicated that the frequently observed groves of *H. oleifolium* were clonal. Because suckering seems strongly dependent on disturbance, it is suggested that simply removing stock will not allow adequate regeneration. Management may need to provide sufficient fire frequency to initiate enough suckers for replacement of old stems and hence stand perpetuation.

A central problem for the management of arid zone vegetation in Australia is the partial or complete failure of some woody species to regenerate (Hall *et al.* 1964, Harrington *et al.* 1984), even though there is still controversy about how many species fall within this category (Stanley 1983, Chesterfield & Parsons 1985). *Heterodendrum oleifolium* (Sapindaceae), 'one of the most useful fodder trees in inland Australia' (Everist 1974), is a species which can fail to regenerate both in the presence of stock (Chesterfield & Parsons 1985) and, in at least some areas, in their absence (Sinclair 1984). The species is widespread in the Australian arid zone (see map in Hall *et al.* 1964). The aim of the present work is to test whether its regeneration both from seed and from root suckers is adequate in the study area and if not, whether grazing by stock is the sole cause of inadequate regeneration.

METHODS

FLOWER AND SEED BIOLOGY

Flower, fruit and seed production was examined at a number of sites several times from February to December, 1985 (Fig. 1, Table 1, Appendix for locations). As dioecy is common in the Family Sapindaceae, this was checked for as a possible aid in identification of clones (see later). All trees checked were monoecious. Seeds were classified as: (a) eaten by insects if seed coats showed characteristic signs of attack; (b) empty, if seed coats lacked such signs but were easily crushed between thumb and finger; or, (c) filled, if coats were filled with white, apparently live, tissue.

Seeds collected from trees between March and August, 1985 were surface sterilized (70% alcohol),

variously treated (Table 2) and tested for germination for 6 weeks 20 per petri dish. It was not realized at the time that the seeds included both empty and filled ones. Germination trials were on Whatman grade 181 filter paper moistened with distilled water in a growth cabinet with 14 h/30°C light cycle and 10 h/15°C dark cycle [high temperature chosen following Burbidge (1960)]. A few trials used constant 26°C instead. The minimum number of replicates used was three (60 seeds).

A final trial, with seeds collected from Red Cliffs on 25 February 1986, used continuous light or continuous darkness at 25°C.

SUCKERING

Detached root pieces

In February, March, May and July, 20-30 cm lengths of lateral surface roots with diameters ranging from 2.5 to 27.5 mm (upper size limit determined by cutting capacity of secateurs) were collected, placed in a mixture of coarse sand, perlite, vermiculite and compost at a depth of 10 cm, put into a Melbourne glasshouse and examined for suckers after 10 weeks.

Seedling damage response

Eighteen month old seedlings were variously (a) decapitated just above soil level, (b) decapitated and treated twice weekly with 1% indole-3-acetic acid (IAA) in lanolin contained in Beem fixing capsules placed over the cut stem, (c) treated as for (b) but using lanolin alone, (d) had all roots severed at a 1 cm radius from the stem to a depth of 3-4 cm, (e) had all leaves removed and (f) left as controls. All plants were placed in a growth cabinet with a 14h/30°C day cycle and 10h/15°C night cycle for 10 weeks.

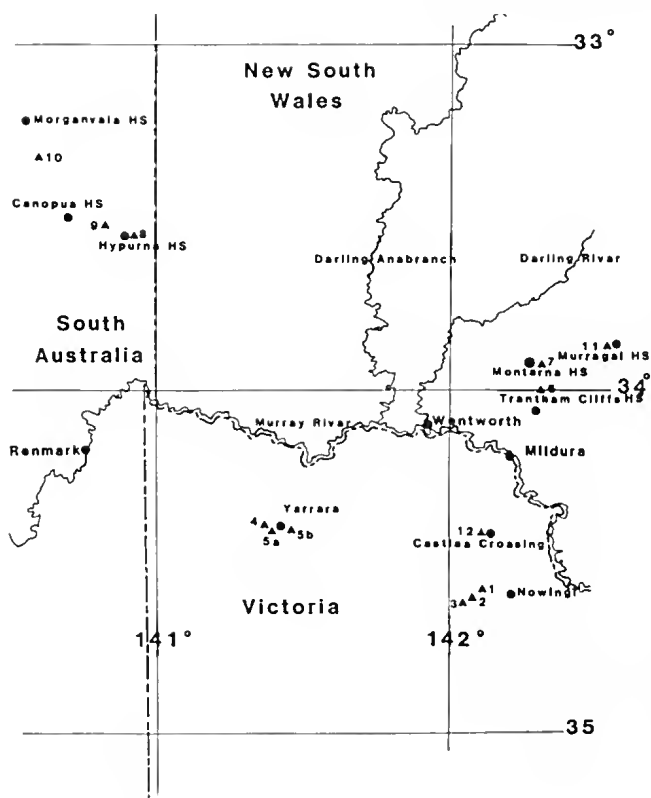


Fig. 1—Location of the study sites.

Field observations

Suckering was examined at sites affected by fire, road grading, stock grazing and ploughing. Stem girth was measured 45 cm above ground level. Throughout the paper, the term 'tree' is used only where stems occur scattered singly and not where stems are clumped to form groves. To sample enough trees, Site 5a was combined with the closely-adjacent Site 5b (Appendix).

TABLE 2
EFFECT OF SEVEN TREATMENTS ON GERMINATION
OF *Heterodendrum oleifolium* AFTER SIX WEEKS
(Data summed across collection dates and temperature
regimes)

Treatment	Number of filled seeds	% germination
Control	80	12
Soaked 2h (water)	9	11
Leached 24h (running water)	21	19
Leached 48h (running water)	19	10

1976). Leaf samples from all stems within each grove were transported to the laboratory on ice, stored at 2°C, and samples (0.5 g) cut up and ground to powder in liquid nitrogen before adding grinding buffer, grinding to paste and the extract clarified by centrifugation. The grinding buffer was that used for buds by Cheliak and Pitel (1984) with the addition of 2.5 mM DIECA, 2 mM sodium metabisulphite and 2 mM sodium tetraborate. The liquid extract was either placed in wells in the gel or absorbed onto filter paper wicks (Whatman 3 mm chromatography paper).

After various trials, the best starch-gel electrophoresis system proved to be 12.5% starch gel containing 0.005 M histidine pH8 gel buffer run with a 0.41 M sodium citrate pH 8 tray buffer. Gels ran for 4 h at 65 mA. Four enzyme systems were examined with the stains used by Fripp (1982).

As well as leaves from the two groves, leaves from various 18 month old seedlings (Forests Commission of Victoria nursery, unknown provenance) were also analyzed to try to encompass material with a wider genetic range.

RESULTS AND DISCUSSION

FLOWER AND SEED BIOLOGY

In February 1985, fertile trees carried mature fruit and not flowers, reflecting the normal, predominantly late spring-early summer flowering time (see also Cunningham *et al.* 1981). Percentage of trees per site flowering and fruiting in the 1984-1985 season varied from 3 at Site 11 to 39 at 12. While some seed was produced in the region in 1984, 1985 and 1986, there was none for several years before that (J.H. Browne & N.G. Aloizos pers. comm., Chesterfield & Parsons 1985), reflecting a widespread tendency for erratic flowering and/or seed set (Burbidge 1960, Hall *et al.* 1964).

The fruits range in size from 5-15 mm diameter and are of one to four locules. Mature seeds (5 mm diameter) are non-endospermic, globose, shiny, black and partly encircled by orange-red arils (Fig. 2). Seed crop data (Table 1) showed that insect larvae (superfamily Pyraloidea, T. New pers. comm.) destroyed up to 68 per cent of seeds present in the crown at any one time. Insect damage occurred at least from February onwards, although it was not quantified until May. The larvae were never found in fruits or seeds beneath the trees (Table 1).

For seeds unaffected by insects, the per cent filled was highly variable and often low (Table 1). While the initial figures could reflect factors like pollen sterility (Haegi & Barker 1985) and parthenocarpy (Gustafson 1942), the data for Site 12 also suggest declining percentages of filled seeds from February to July. This reduction could involve factors like insect-introduced fungal diseases (as in *Pistacia*, Jaynes 1979), seeds being innately short-lived (Mayer & Poljakoff-Mayber 1982), drying or heating effects on viability or even selective removal of filled seeds from crowns by birds or insects. Very few filled seeds were found on the soil surface (Table 1); it is

not known whether removal of filled seeds by ants contributes to this. By July, filled seeds were scarce both on the soil surface and in the crowns. However, some trees were exceptional; at Nowingi as late as 19 August 1985, amongst many *Heterodendrum* trees lacking seed, a single tree was found carrying a large seed crop. Of the seeds unattacked by insects, 20% were filled.

Some preliminary work suggests that, in the crown, the arillate seeds in open fruits were much more likely to be filled than seeds from undehiscent fruits at any given time.

When the germination experiments were set up, the low percentage of filled seeds had not been recognized. Filled seeds were so few that the results are preliminary only and statistically unanalyzable. Those presented (Table 2) are summed across collection dates and the two temperature regimes, as these had no apparent effect. Seed nicking appeared to enhance germination (Table 2), suggesting that some seeds had an impermeable testa as is known for other species in this family (Floyd 1966). The germination of a few untreated seeds (Table 2) suggests that some 'soft' seeds are present in seed batches less than one year old. Germination is epigeal.

The 1986 seed sample had a high percentage of seeds held in very recently-opened fruits. It showed that high germinability is possible with scarified fresh seed and confirmed the occurrence of hard-seededness (Table 3).

It is clear that problems of spasmodic flowering, seed emptiness, seed predation by insects and low germinability occur. The spasmodic flowering and apparent rapid decline in seed viability with time strikingly resemble the behaviour of *Acacia harpophylla*, another root-suckering species (Johnson 1964).

SUCKERING

Transverse sections showed that the horizontal, sub-surface organs from which suckers often arise are in fact roots.

Detached root pieces

No root suckers formed on any of the detached root pieces. Swellings of callus tissue on both damaged and undamaged surfaces occurred on some pieces of 3 to 21 mm diameter. It is not known if these were precursors to roots or shoots. Some pieces produced young roots which did not arise from swellings. In *Populus*, root suckers may occur in as little as two weeks but are common within seven weeks from excision (Farmer 1962, Sehler 1972).

Seedling damage response

After 10 weeks, the decapitated plants had produced sucker shoots from the cut section. Those decapitated then treated with IAA and lanolin gave no response but neither did 7 out of 10 of those given only lanolin, possibly because IAA and lanolin were added by pouring into Beem fixing capsules fitted over the stumps. The capsules may have prevented stem suckers from developing. Root severance produced swellings of callus

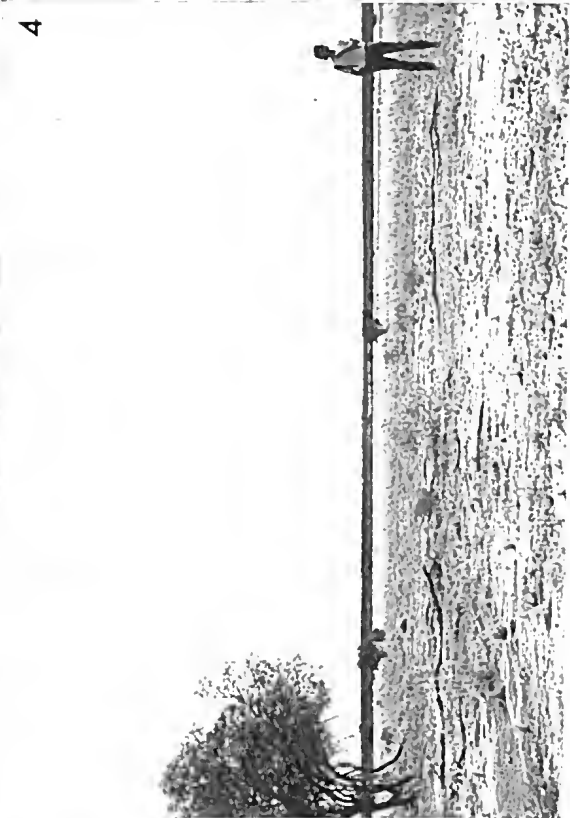
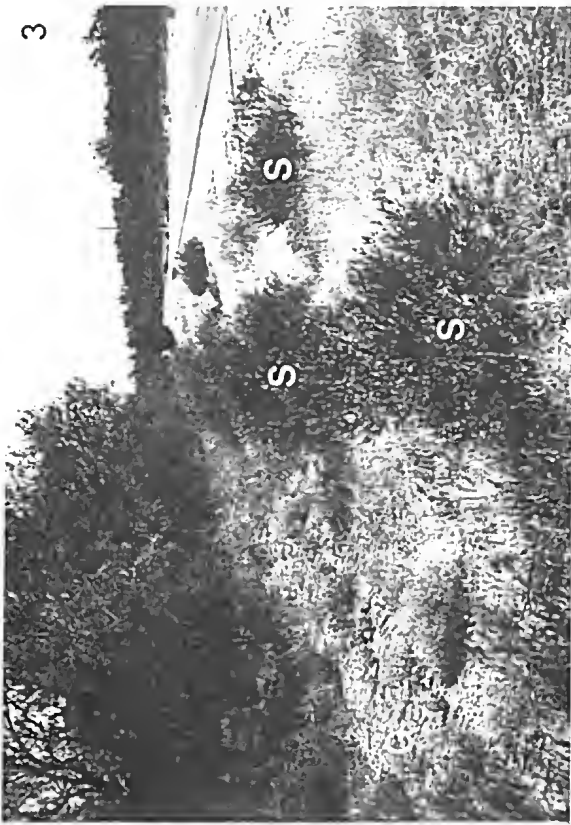


Fig. 2—Mature seed of *Heterodendrum oleifolium* partly enclosed by aril (A), showing the funicle (F) and the hilum (H).
× 2.4.

Fig. 3—Adult stems of *Heterodendrum oleifolium* (upper left) and road verge at Site 5 showing edge of grader scrape (G) and line of *H. oleifolium* root suckers to 1 m high (S) within scraped area. Note absence of suckers in undisturbed area to left of scrape.

Fig. 4—Adult stems of *Heterodendrum oleifolium* 6 m high with exposed lateral roots 15 m long bearing suckers. Former stock holding paddock, Site 8.

Fig. 5—*Heterodendrum oleifolium* suckering after 1975 fire, Site 6. Arrowed from right to left are (a) adult parent trunk and crown killed by the fire (b) grazed sucker 90 cm high 3.5 m from trunk and (c) ungrazed sucker 1.7 m high 8.2 m from trunk. (a), (b) and (c) are in a line and are very likely to be part of one individual. Live tree in centre is *Casuarina cristata*.

TABLE 3

EFFECT OF THREE TREATMENTS ON PERCENTAGE GERMINATION OF 1986 *Heterodendrum oleifolium* SEED AT 25°C.
All values based on 100 filled seeds per treatment

Treatment	Time	
	7 days	19 days*
Control	8	19
Nicked, continuous light	38	88
Nicked, continuous darkness	82	93

* All germination had ceased after about 30 days.

tissue on both attached and detached roots, some initiation of new roots and also, a single root sucker distal to the point of severance. The sole response to leaf removal was rapid growth and leaf production by axillary buds.

Taken overall, the results show considerable resilience to severe damage in 18 month old seedlings. The responses to decapitation and defoliation are consistent with views that these treatments reduce the flow of auxin and remove the inhibition to preformed dormant buds (Farmer 1962, Eliasson 1969). In the present case, it is usually dormant stem buds that become active; these may re-establish apical dominance thus preventing any development of root buds and hence of root suckers.

Field observations

Despite detailed search, no root suckers were found at any undisturbed site. Excavation showed that suckers usually arose from lateral roots from 2 to 15 cm deep. Where roots were severed by ploughing, all resulting suckers developed only on the severed root but not necessarily close to the point of severance (Table 4). All suckers produced after road grading were in the graded area clear of the undisturbed area (Fig. 3), suggesting the same effect. Such distal sucker production also occurs in *Populus tremuloides* and *Liquidambar*

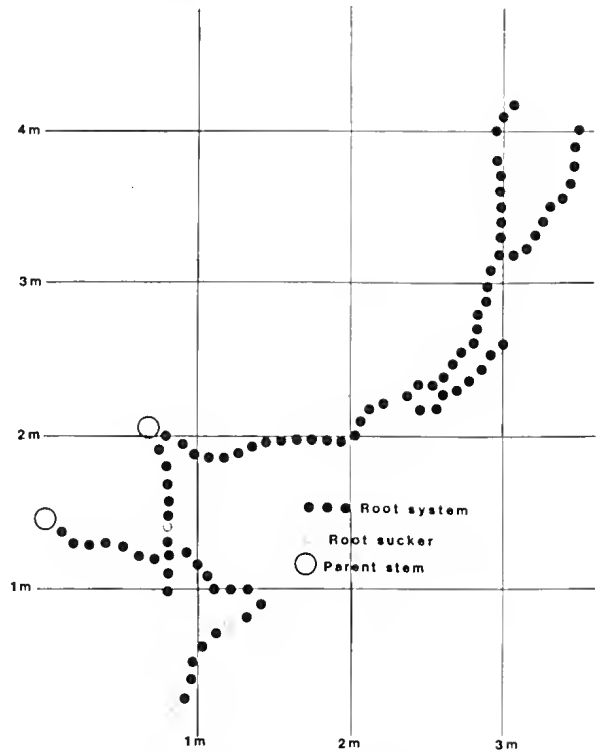


Fig. 6—Plan diagram of suckering *Heterodendrum oleifolium* root systems, Site 6.

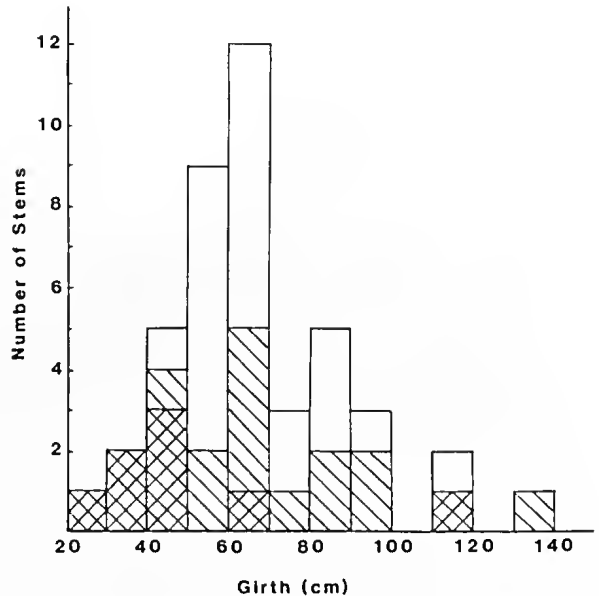


Fig. 7—Girth histogram for *Heterodendrum oleifolium* at Site 6 showing responses to the 1975 wildfire. Cross-hatching shows trees killed by fire, diagonal hatching shows trees producing root suckers after fire, no hatching shows live trees without root suckers.

TABLE 4
RELATIONSHIP OF DISTURBANCE TO ROOT SUCKERING IN *Heterodendrum oleifolium*

Site	History	Number of root suckers per adult stem*	Observations
1	Ploughing	26	Suckers distal to site of root severance
5	Road grading	21	Not excavated. See text
8	Stock holding yard	0.2	Suckers arising from damaged roots exposed by erosion
6	Wildfire 1975	1	Suckers present on undamaged roots
10	Wildfire 1984	0.5	Suckers present on undamaged roots

*Mean values. Sample size from three to 699.

styraciflua and suggests that root suckering is controlled by the shoot apex (Farmer 1962, Kormanik & Brown 1967).

At site 8, exposed lateral roots 15 m long were attached to adult stems 6 m high (Fig. 4). Topsoil erosion here probably followed overstocking. Suckers occurred both on broken and unbroken roots. It is not known if the latter had been damaged (e.g. by hoofs). Site 6, is thought to have been burnt by a high intensity wildfire in 1975. Nineteen per cent of mature *Heterodendrum* trees were killed outright, mostly smaller trees of less than 50 cm girth (Fig. 7). It seems very likely that root suckering sometimes occurred on plants whose main stem was killed by fire (Fig. 5) but more usually on plants whose main shoot system eventually recovered and produced a new crown. The root suckers were up to 8.2 m from the parent stem (Fig. 5). Thirty per cent, in a range of sizes, formed root suckers, while 51 per cent either showed no obvious damage 10 years later or had a few epicormic shoots usually at the base of the trunk. At this site, excavation around mature, burnt stems of *Heterodendrum oleifolium*, revealed surface roots with suckers more than 3 m from the parent stem and showed how closely adjacent suckers can arise from different parent stems on intersecting roots (Fig. 6). Although these suckers are now approximately 10 years old, their average height is only about 30 cm. Examination suggests that this is caused by stock grazing. The only large sucker found was 1.7 m high (Fig. 5) and was flowering for the first time. Little is known of normal rates of height growth.

Finally, site 10 had been burnt by wildfire in December 1984. Burnt *Heterodendrum* had not regenerated by August 1985 (possibly hindered by low rainfall) but some had done so by December of that year. Strikingly, the fire completely destroyed all aerial plant parts over large areas of mallee vegetation, but rapidly went out once it reached the different fuel conditions of the *Casuarina cristata*-*Heterodendrum oleifolium* woodland, where it damaged only a few marginal trees. Only 12 such *H. oleifolium* trees could be found along a fire boundary of at least 6-7 km. Of these, five appeared to have been killed outright and four had epicormic shoots in the crown and/or the main trunk but lacked root suckers. Of the three with root suckers, two had totally dead main trunks.

There was no evidence of continuous variation in sucker size or age at any site. All root suckering seen initially could be readily related to specific disturbance events and so was considered episodic. The only records of *Heterodendrum* root suckering without obvious disturbance are those of Hall *et al.* (1964) and of Chesterfield and Parsons (1985) at their Site 5. While re-examination of the latter indicated no obvious disturbance, possibly past defoliation by drought, insects etc. could provide the stimulus for sucker initiation. There is a range of views on the role of disturbance in root suckering in other species. For example, in *Populus*, Farmer (1962) stressed the importance of removing inhibition by the shoot apex before root suckering will begin, while Barnes (1966) and Cook (1983) strongly implied that *Populus* clones can develop gradually by suckering of a continually expanding root system without any damage to shoots or roots. Moar (1955) stressed that *Dacrydium colensoi* in New Zealand will root sucker without disturbance and treated this as the accessory type of suckering (part of normal development) compared to the reparative type (sequel to root injury or shoot destruction).

CLONAL GROWTH HABIT

Girth measurement

At both sites, stems of *Heterodendrum oleifolium* of less than 20 cm girth were absent (Figs. 8 & 9) other than some small root suckers at Site 8. Both histograms may represent single normal distributions as could be caused by a single suckering episode. The larger girths at Site 3 could relate to some combination of site conditions, lower stem density or greater age. There were no signs of large, old, possibly parental stems or stumps in the middle of or near the groves.

Maximum grove diameters at Sites 3 and 8 were 28 m (17 stems) and 18 m (28 stems) respectively (Fig. 9).

Isoenzyme analysis

All samples showed the same two-banded pattern for the glucosephosphate isomerase system. For the other enzyme systems, while each grove was invariant, Sites 3 and 8 were completely different. Further variability was seen in the seedlings (Fig. 10). Such invariance within groves combined with clear isozyme differences from other provenances strongly suggests a clonal origin for

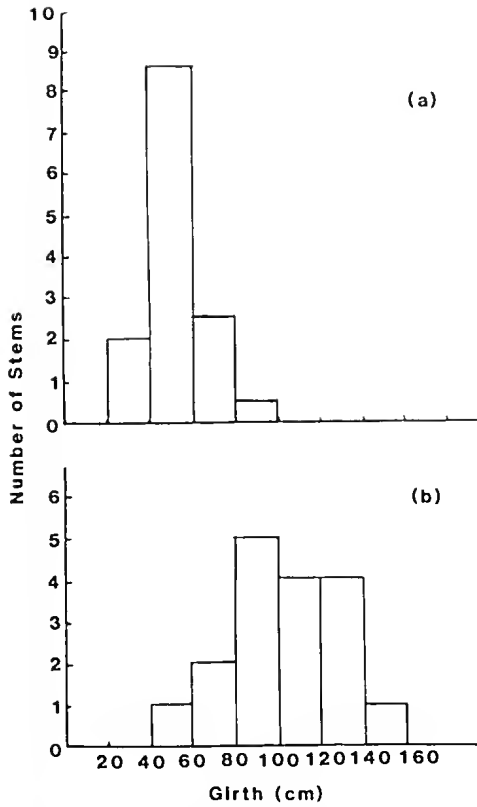


Fig. 8—Girth histograms for groves of *Heterodendrum oleifolium*. (a) At Site 3. (b) At Site 8.

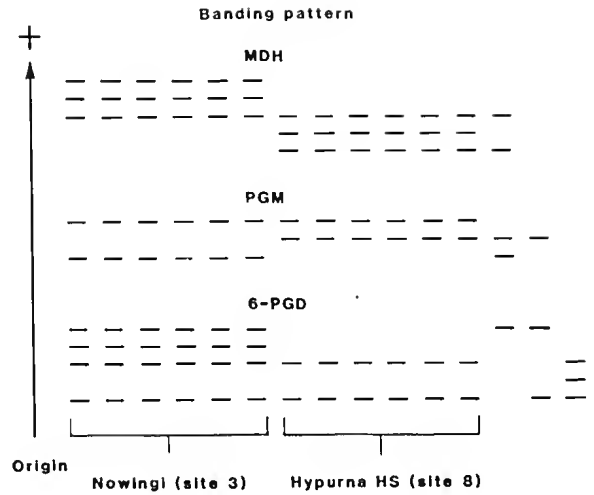


Fig. 10—Representative zymograms for three enzyme systems for six mature stems at Site 3, six at Site 8 and three seedlings. Every banding pattern shown was found in at least one seedling. MDH=malate dehydrogenase, PGM=phosphoglucosmutase, 6-PGD=phosphogluconate dehydrogenase.



Fig. 9—The analyzed *Heterodendrum oleifolium* grove 6 m high and 28 m across at Site 3. Note browse line maintained by sheep at about 75 cm above ground.

the groves (Sternberg 1976, Huenneke 1985), supporting previous suggestions to that effect (Hall *et al.* 1964, Beadle 1981). While maximum clone size documented was 28 m diameter, analyses are needed over larger areas. For example, at Site 8, large patches of *Heterodendrum oleifolium* very close to the grove analyzed could possibly all have constituted a single clone at least twice that size. In *Populus tremuloides*, clone size can reach 47,000 stems over 43 ha (Cook 1983).

Clonal growth may be significant in semi-arid and arid areas because it minimizes the necessity for seedling establishment and may, by continuous rejuvenation, increase longevity up to the point of virtual or absolute immortality (Muller 1951, Noble 1986). In the present work, it was not possible to find senescing mature stems to see if senescence can initiate sucker formation. Immortality or even great longevity should not be assumed under present conditions given widespread death of old stems of *Heterodendrum* without replacement at Koonamore (Hall *et al.* 1964, Sinclair 1984). Potentially, death of mature stems could be accompanied by cessation of suckering and death of root systems.

The present girth data are consistent with the idea of root suckering and clonal growth being caused by episodic events of which fire may be the most likely.

CONCLUDING DISCUSSION

Overall, the data suggest that flowering and seed characteristics of *Heterodendrum oleifolium* make seedling establishment difficult and therefore rare. The species could often survive damage by fire and other agencies by producing root suckers and epicormic shoots.

The present work is consistent with previous findings that *H. oleifolium* will not regenerate adequately from suckers where stock are present (Chesterfield & Parsons 1985). However, the recommendation that simply spelling from stock will allow regeneration from suckers (Chesterfield & Parsons 1985) may need modifying. *H. oleifolium* may be so strongly dependent on damage by fire or other agencies for the initiation of suckering and clonal growth that just removing stock will not be sufficient. It is thus important to know the fire frequency required to permit replacement of stems by new suckers, since the intervals between fires may exceed 50 years (Hodgkinson & Harrington 1985). Management of *Heterodendrum* populations may therefore require not only control of mammal browsing but also the regular incidence of a disturbance agent like fire may be needed to ensure sucker initiation, sucker protection and stand perpetuation.

ACKNOWLEDGEMENTS

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APPENDIX

LOCATION OF STUDY SITES

Site no.	Grid reference*	Details
1	XG 080 710	Nowingi, tree in recently ploughed paddock
2	XG 072 708	Nowingi, grazed by stock, otherwise undisturbed
3	XG 005 704	Nowingi, grazed by stock, otherwise undisturbed
4	WG 355 935	Yarrara, undisturbed
5a	WG 356 933	Yarrara, cleared by road grader
5b	WG 401 924	Yarrara, cleared by road grader
6	XH 246 217	Trentham Cliffs, burnt by 1975 wildfire
7	XH 302 257	Montarna, undisturbed
8	393 853	Hypurna, former stock holding yard
9	386 857	Hypurna, undisturbed
10	359 879	Canopus, burnt by 1984 wildfire
11	142° 52' north-33° 52' east	Murragai, trees in recently ploughed paddock
12	XG 105 820	Castle's Crossing Bushland Reserve, undisturbed

* Grid references from 1:100,000 topographic maps except for sites 8-10 (1:250,000) and 11 (1:1,000,000)

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STUDIES ON WESTERN AUSTRALIAN PERMIAN BRACHIOPODS

6. THE GENERA *STROPHALOSIA* KING, 1844, *HETERALOSIA* KING, 1938 AND *ECHINALOSIA* WATERHOUSE, 1967.

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ABSTRACT: Strophalosiid brachiopods of the genera *Strophalosia*, *Heteralosia* and *Echinalosia* from the Permian sequences of Western Australia are revised and described. The new subgenus *Notolosia* is diagnosed and the following species described: *Strophalosia irwinensis* Coleman, *Strophalosia jimbaensis* sp. nov., *Heteralosia etheridgei* (Prendergast), *Heteralosia prendergastae* (Coleman), *Heteralosia compleciensis* (Etheridge), *Echinalosia prideri* (Coleman) and *Echinalosia (Notolosia) dickinsi* subgen. et sp. nov. Additional material belonging to *Strophalosia* and *Heteralosia* is briefly described and figured.

The classification of the superfamily Strophalosiacea is briefly discussed, the Ctenalosiinae of Muir-Wood and Cooper (1960) is raised to family status as the Ctenalosiidae and the new subfamily Licharewiellinae is proposed within the Strophalosiidae Schuchert (1913).

Strophalosiid brachiopods are abundant in the marine Permian faunas of Western Australia. This paper continues the series of studies on Western Australian Permian brachiopods (Archbold 1985) and documents representatives of the genera *Strophalosia*, *Heteralosia* and *Echinalosia*. The remainder of the Western Australian representatives of the family Strophalosiidae will be described in a subsequent study. Strophalosiids described herein come from various stratigraphical horizons within the Perth, Carnarvon and Canning Basins. The stratigraphy of these basins is documented in references referred to in Archbold (1981, p. 109) and the basis for age assignment of species is the same as that utilised in recent studies of Western Australian spiriferid brachiopods (Archbold & Thomas 1985). Terminology is standard as in previous studies.

Several of the species described are useful for inter-basinal correlation, notably *Strophalosia irwinensis*, *Heteralosia etheridgei* and *Heteralosia compleciensis*, while all other species are useful for intrabasinal correlations.

The terminology used herein follows that used by Muir-Wood (1965) and Sarycheva (1970).

COLLECTIONS

All figured and measured specimens are housed in the following institutions as indicated by the prefix to the registered numbers. CPC—Commonwealth Palaeontological Collections of the Bureau of Mineral Resources, Geology and Geophysics, Canberra, A.C.T. GSWA—Geological Survey of Western Australia, Perth, Western Australia. MUGD—Department of Geology, University of Melbourne, Parkville, Victoria. UWA—Department of Geology, University of Western Australia, Nedlands, Western Australia. AMF—Australian Museum, Sydney, New South Wales.

All figured specimens of new species, other than holotypes are paratypes.

SYSTEMATIC PALAEONTOLOGY

Order PRODUCTIDA Sarycheva & Sokolskaya, 1959

Suborder STROPHALOSIIDINA Waterhouse, 1975

Superfamily STROPHALOSIACEA Schuchert, 1913

DIAGNOSIS: Strophalosiidinae with hinge teeth or denticles in the ventral valve and sockets in the dorsal valve. Ventral valve with well-developed interarea with pseudodeltidium closing delthyrium. Dorsal valve with low interarea. Ventral valve usually cemented by umbonal region and often with rhizoid spines on ears and slopes. Dorsal valve with or without spines. Cardinal process bilobed in primitive genera, trilobed in advanced genera. One family lacking interareas and teeth and sockets (Teguliferinidae).

DISCUSSION: The diagnosis is largely based on Muir-Wood and Cooper's (1960) understanding of the Strophalosiidae. Waterhouse (1978a) included the Strophalosiidae Schuchert, 1913; Teguliferinidae Muir-Wood and Cooper, 1960; and the Hercosiidae Cooper and Grant, 1975 within the Strophalosiacea. It would appear preferable to leave the Hercosiidae within the Riebhofeniacea as intended by Cooper and Grant (1975, p. 928) and the Teguliferinidae may also be better placed in the Riebhofeniacea. Nevertheless the Teguliferinidae possess an erect "*Strophalosia*" type of cardinal process and a distinctive growth form of the ventral valve (Muir-Wood & Cooper 1960, p. 93). As a result I retain the family within the Strophalosiacea.

The subfamily Ctenalosiinae Muir-Wood and Cooper (1960) would appear to deserve family status, because of the distinctive development of ventral denticles and corresponding dorsal pits, and hence is raised to family status, as the Ctenalosiidae, herein. The Ctenalosiidae is diagnosed as Strophalosiacea with numerous ventral denticles and corresponding dorsal pits along the hinge. The genera *Ctenalosia* Cooper and

Stehli (1955) and *Mongolusia* Manankov and Pavlova (1976) are included within the family. The two genera are of strikingly-dissimilar external ornament and size and yet both possess denticles and multiple sockets. The two genera do not appear closely related and hence the origin of the Ctenalosiidae is obscure but it appears unlikely that the unusual denticulate hinge line could have evolved independently in the two genera.

Family STROPHALOSIIDAE Schuchert, 1913

DIAGNOSIS: Strophalosiaceans with ventral hinge teeth and dorsal sockets. Interareas distinct. Ventral valve usually cemented by umbonal region and often with rhizoid spines on ears and slopes. Dorsal valve with or without spines. Cardinal process bilobed, trilobed or quadrilobed.

DISCUSSION: The subdivision of this family has been the subject of extensive discussion. With the establishment of *Strophalosia gerardi* King, 1846 as the type species of *Strophalosia* King, 1844 (I.C.Z.N. 1962, Opinion 625), nomenclatural stability has occurred within the family. The morphological characters of *Strophalosia gerardi* are discussed under the generic heading.

Hall and Clarke (1892, p. 316) delineated stocks of *Strophalosia* by means of the external ornament of the dorsal valve. They noted that there were species attributed to *Strophalosia* with spiniferous, lamellose or smooth dorsal valves. Muir-Wood and Cooper (1960) recognised two subfamilies dependent on the nature of the dorsal exterior ornament: the Strophalosiinae Schuchert with dorsal spines; the Heteralosiinae Muir-Wood and Cooper without dorsal spines. Because of the clarification of the morphology of the type species of *Strophalosia*, which lacks dorsal spines, Brunton (1966) redefined the Strophalosiinae as forms without dorsal spines and established the subfamily Dasyalosiinae Brunton for those genera with dorsal spines. This recasting of subfamilies has been reviewed by Clarke (1970a) and Cooper and Grant (1975). Cooper and Grant (1975, p. 195) considered *Heteralusia* to be generically distinct from *Strophalosia*, a view adhered to herein, but they did not diagnose the distinction. Irrespective of whatever criteria are used to define subfamilies within the Strophalosiidae it appears difficult to classify *Heteralusia* and *Strophalosia* into separate subfamilies and hence the Heteralosiinae should be permitted to lapse. Grant (1976, p. 80) continued to use the Heteralosiinae without a discussion of the arguments presented by Brunton (1966) and other authors or a comparison of *Heteralusia* with *Strophalosia*.

Waterhouse (1964, 1969) and Clarke (1970a) have accrued data which questions the value of dorsal valve spinosity as a criterion for subdividing the family. As a result I follow those authors in not employing dorsal valve spinosity as a criterion for splitting the family. This is also consistent with views indicated by Grigor'eva (1977) and Chang and Ching (1976). For the present I include the following subfamilies within the Strophalosiidae, namely Strophalosiinae Schuchert, 1913; Mingceniinae Archbold, 1980 and Licharewiellinae

subfam. nov. The peculiar nature of the Mingceniinae was discussed by Archbold (1980b). The new subfamily Licharewiellinae is formally proposed here and is diagnosed as Strophalosiidae with an external ornament of coarse costae and variably-developed dorsal spines. Genera included within the Licharewiellinae are *Licharewiella* Ustritskiy (in Ustritskiy *et al.* 1960), which is an objective senior synonym of *Costalosia* Waterhouse and Shah (1966), *Costalosiella* Waterhouse (1983) and *Australusia* McKellar (1970). The presence of coarse costae is a feature of all genera.

Licharewiella was placed by Wang *et al.* (1966, p. 439) in the Aulostegidae Muir-Wood and Cooper, without discussion. Liao (1982, p. 539) included *Licharewiella* within his new subfamily Truncateninae within the Aulostegidae. However, description of Salt Range and Tasmanian *Licharewiella* (including the type species) by Waterhouse and Shah (1966) and Clarke (1970a) respectively, indicates a firm strophalosiid affinity for the genus. The internal structures of the Salt Range Licharewiellinae are poorly known but Tasmanian evidence (Clarke 1970a) indicates a firm strophalosiid relationship for the group.

Australusia McKellar (1970) from the Latest Devonian of Queensland, possesses well-developed, coarse, branching costae on both valves and is possibly ancestral to Permian members of the subfamily.

Subfamily STROPHALOSIINAE Schuchert, 1913

DIAGNOSIS: Strophalosiids with ventral valve normally cemented by umbonal region of ventral flank and often with rhizoid spines on ears and on flanks. Dorsal valve spinose, lamellose or smooth, may be capillate and pitted. Cardinal process bilobed, trilobed or quadrilobed.

DISCUSSION: This is a large subfamily of over 20 genera. The constituent genera have been well reviewed by Muir-Wood and Cooper (1960) or have been clearly diagnosed by subsequent authors. This paper describes representatives of the genera *Strophalosia* King (1844), *Heteralusia* King (1938) and *Echinosia* Waterhouse (1967) from the Western Australian Permian. Relevant genera are compared with these genera below and additional Western Australian Permian Strophalosiinae will be described in a subsequent paper.

Genus *Strophalosia* King, 1844

TYPE SPECIES: *Strophalosia gerardi* King, 1846, from the Permian of Ladakh (Indian Himalayas), horizon unknown.

DISCUSSION OF TYPE SPECIES: The holotype of the species (Galway University College, FC, D.267) has been figured by King (1850, pl. 19, figs 6-7), Davidson (1853, pl. 8, fig. 211), Hall and Clarke (1892, pl. 17, fig. 50), Prendergast (1943, pl. 5, figs 13, 16-17) and Brunton (1966, pl. 1, figs 8-9). Only Prendergast figured a profile of the holotype. Brunton also figured an additional specimen from the Himalayas (1966, pl. 1, fig. 7), the specimen having, presumably, also been collected by Dr J. G. Gerard during his Himalayan expeditions.

The Himalayan expeditions of Surgeon J. G. Gerard of the Bengal Native Infantry resulted in several collections of fossils being sent down from the Himalayas. These fossils attracted considerable attention at the meetings of the Asiatic Society of Bengal with brief notes being written on some of the specimens and their locations (Everest 1831, 1833, Herbert 1831). Specimens were sent to England and commented upon briefly by J. deC. Sowerby (1832, 1833). Letters were also sent to the Asiatic Society by Gerard giving details of the fossil discoveries (Gerard, 1831) and who subsequently provided a large paper on the Spiti Valley region (Gerard, 1833). He was to have provided a second paper detailing the geological settings of his fossil discoveries (note to Gerard's 1833 paper by James Prinsep, Secretary to the Physical Class of the Asiatic Society of Bengal). However, the second paper does not seem to have eventuated. At least it is not referred to by Royle (1840), a valuable reference detailing much of the geological exploration of the Himalayas by that time. Royle (1840, pl. 3, figs 16-27) figured additional specimens collected by Gerard, one of which (op cit. pl. 3, fig. 23) may be allied to the Permian spiriferid genus *Trigonotreta*, again indicating that Gerard collected from Permian strata. For the time being the best indication of the locality of the type specimen is that given by Gerard (1833, p. 276-7) and repeated by King (1850, p. 96), namely "just before crossing the boundary of Ladakh into Basahir, I was gratified by the discovery of a bed of marine fossil shells resembling oysters, and clinging to the rock in a similar manner, but the suspicions of the Chinese prevented my bringing away many specimens. The loftiest position at which I actually picked up some of the shells was on the crest of a pass elevated 17,000 feet, where also were seen numerous blocks of calcareo-siliceous matrix" (Gerard 1833, p. 276-7). It is quite possible that other letters and perhaps maps were transmitted to the Asiatic Society of Bengal by Gerard and that an investigation of the old records of the society, if extant, may provide further information.

GENERIC DIAGNOSIS: *Strophalosiinae* with erect and recumbent spines over ventral valve. Dorsal valve with no spines, delicate concentric lamellae and delicate impersistent capillae. Shell shape usually subcircular.

DISCUSSION: The generic name *Strophalosia* was introduced by King (1844, 1845) and diagnosed later (1846, 1847). *Strophalosia gerardi* was described by King in 1846 and hence was the only species available as type species of the genus (I.C.Z.N. 1962, Opinion 625).

Coronatosia Waterhouse and Gupta (1978) (type species *Coronatosia blijniensis* Waterhouse & Gupta 1978) is morphologically closest to *Strophalosia*. It differs most obviously in the presence of a row of hinge spines that are sturdy and open into the interior of the valve into late maturity. Waterhouse and Gupta (1977, p. 14; 1983a, pp. 125) have used the name *Arclmaelosia*, a *nomen nudum*, which apparently refers to *Coronatosia*, a genus validly described in 1978.

Waterhouse and Gupta (1978, p. 417) noted that the dorsal exterior of *Strophalosia gerardi* is covered with

prominent pits (or dimples) and pustules, as well as lamellae and traces of radial capillae and hence is similar to the dorsal valve of *Strophalosia subcircularis* Clarke (1970a) which is also covered with well-defined radial capillae according to those authors. Fine intermittent capillae occur on the dorsal valve of well-preserved specimens described herein and referred to *Strophalosia irwinensis* Coleman.

As noted by Brunton (1966), *Strophalosia* is similar morphologically to *Heteralosia* King 1938, a genus discussed below. Cooper and Grant (1975, p. 795) considered *Heteralosia* to be distinct from *Strophalosia*. However, they did not diagnose either genus. Their species *Strophalosia inexpectans*, is atypical for the genus *Strophalosia* and indeed the presence of fine, recumbent, hair-like spines on the dorsal valve precludes the species from *Strophalosia*. The species *Strophalosia inexpectans* possesses such delicate spines on both valves that it does not fit readily into any described strophalosiid genus. Grant (1976, p. 80) gave a detailed diagnosis of *Heteralosia* but did not compare the genus with *Strophalosia*. Nevertheless, *Heteralosia* is regarded herein as a distinct genus and is discussed further below.

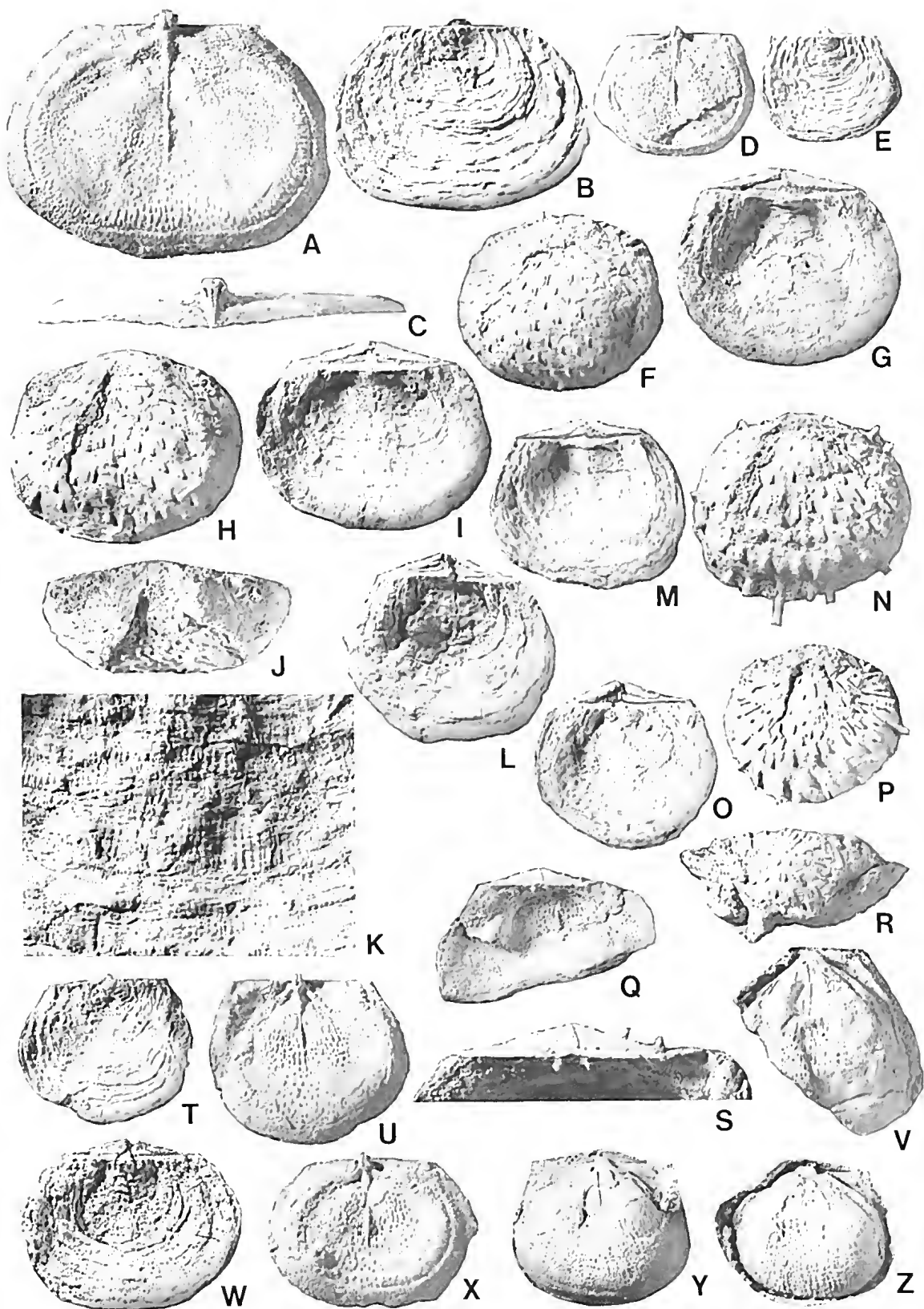
Strophalosia is reliably known from early Permian faunas of Tasmania (Clarke, 1970a), New South Wales and Queensland (Waterhouse, *et al.* 1983) and Western Australia. Artinskian species are known from the Salt Range, Pakistan (in the forms of *S. tenuispina* Waagen, 1884 and *S. sublamellata* Reed, 1944). Late Permian species are known from the Himalayas (Waterhouse, 1983) and the Karakorum (Waterhouse & Gupta, 1983b), although, like *S. gerardi*, the age of which is not known, these species are relatively poorly known. Early Late Permian species such as *S. sibirica* Licharew (1934a) from northern and northeastern Siberia, Arctic USSR, appear to be true *Strophalosia* species (Grigor'eva, 1977). In the Soviet Arctic, the genus appears to occur as far west as Novaya Zemlya (Kalashnikov & Ustritskiy, 1981) and then as far south as the Kamian Priurals in the form of the Sakmarian *Strophalosia striatotuberculata* (Mirskaya *et al.* 1956).

Strophalosia irwinensis Coleman, 1957

Figs 1A-Z, 4A-I

- 1943 *Strophalosia* sp. cf. *gerardi*: Prendergast, p. 46; pl. 5, figs 14-15.
- 1943 *Strophalosia tenuispina*: Prendergast, p. 52; pl. 6, fig. 9.
- 1957 *Strophalosia (Heteralosia) irwinensis*: Coleman, p. 122; pl. 20, figs 1-6.
- 1957 *Strophalosia (Heteralosia) tenuispina*: Coleman, p. 130; pl. 20, figs 36-37.
- 1967 *Strophalosia prideri*: Condon, p.70
- 1976 *Strophalosia (Heteralosia) irwinensis*: Coleman; Playford *et al.*, p. 95.

HOLOTYPE: UWA 23441a, a ventral valve from Fossil Cliff, Irwin River; Fossil Cliff Member of the Holmwood Shale, Perth Basin. Figured by Coleman (1957, pl. 20, figs 1-2).



MATERIAL, LOCALITIES AND AGE: Specimens as figured and measured in addition to abundant material from the Callytharra Formation collected by Dr G. A. Thomas, University of Melbourne. MUGD F6577, 6581, 6587, 3 isolated dorsal valves from G. A. Thomas locality PB 610, from measured section at 539 m bearing 290° from junction of Bilung Creek and Wooramel River, 75.5 m above base, Callytharra Formation. MUGD F6582, 6578, 6586, 2 conjoined shells and one ventral valve from G. A. Thomas locality PA 591, same section as above, 54.5 m above base, Callytharra Formation. MUGD F6590, an isolated dorsal valve from G. A. Thomas locality X813, from measured section, 2.5 km west of Coordwandu Homestead, at 8.5 m above base, Callytharra Formation. MUGD F6593, a conjoined shell from G. A. Thomas locality P 498, type section of Callytharra Formation, Callytharra Springs, 34-38 m above base of section. MUGD F6591, 6594, 1 conjoined shell and 1 isolated ventral valve from G. A. Thomas locality P 501, same section as P 498, 42-43 m above base of section. MUGD F6592, 6595, 2 conjoined shells from G. A. Thomas localities Q 550 and Q 545, from measured section on a creek near Gap Pool, Wooramel River, 4.6 km bearing 333° from Kcogh Hill, Wooramel River District, 56 m and 42.5-46 m above base of section respectively, Callytharra Formation. All Carnarvon Basin. All Sterlitamakian (Late Sakmarian).

CPC 24429-24430, 2 ventral valve internal moulds from BMR locality TK5A, Scott Bluff, east side of Lake Blanche, southern Canning Basin, Cuncudgerie Sandstone. Sterlitamakian (Late Sakmarian).

Specimens from the Sterlitamakian Fossil Cliff Member of the Holmwood Shale (Perth Basin) were well figured by Coleman (1957, pl. 20, figs 1-6).

SIZE RANGES: A total of 44 specimens (including the figured specimens) were measured. Hinge width, 5.6-23.8 mm; maximum width, 7.5-32.8 mm; ventral valve height, 6.9-24.6 mm; dorsal valve height, 6.1-22.5 mm; thickness, 2.1-8.3 mm.

DIAGNOSIS: Small to medium sized *Strophalosia*; moderately-convex ventral valve; gently-concave dorsal valve in early stages of ontogeny, moderately-concave dorsal valve in maturity. Dorsal valve with ill-defined dimples, well-developed growth lamellae, radial capillae and no spines. Ventral valve with row of hinge spines and variably-defined rows of body spines; spines low angled and recumbent. Cicatrix of variable size.

DESCRIPTION: Shell small to medium sized, transversely oval or subcircular in outline. Hinge width varies from 0.6 of maximum width to 0.9 of maximum width. Hinge extremities rounded or finely pointed. Convexity of ventral valve relatively even with a slight increase in convexity over visceral disc. Gentle median depression or sulcus present in a few specimens but dies out before anterior margin of valve. Umbo not prominent, usually cemented to substrate. Cicatrix varies from small, barely recognisable to large (maximum size 10.9 mm wide), prominent; reflecting variable duration of attachment for juveniles of species. Dorsal valve flat to gently concave in juveniles, becomes more distinctly concave in mature individuals. Ventral interarea prominent, relatively high, gently concave or flat, finely-striated parallel to hinge line. Delthyrium small, high, narrow, filled with small, gently-convex pseudodeltidium. Dorsal interarea distinct, relatively high, bisected by small, narrow, high, triangular notothyrium filled by gently-convex chilidium. Dorsal interarea inclined at up to 30° to cardinal process or may be close to coplanar with the process.

Ornamentation of ventral valve consists of scattered spines, at times showing concentric and subquincuncial arrangement. Spines relatively coarse along cardinal margin and anterior portion of mature specimens, being up to 1 mm thick at bases. Body spines vary from recumbent to projecting anteriorly at low angle to valve. Hinge spines erect, point away from umbo; arranged as single row along cardinal margin and over ill-defined, small ears. Ventral valve also possesses widely-spaced, distinct, concentric growth lamellae.

Dorsal valve lacks spines but possesses prominent, concentric growth lamellae, low, fine, radial capillae between the lamellae (about 3 per mm at 1.8 cm from umbo) and a few scattered, shallow, elongate dimples on a minority of specimens. Many specimens lack dimples entirely.

Ventral interior possesses distinct, but small, diverging teeth. Muscle marks clearly shown on internal moulds; adductor scars relatively small, smooth and bisected by low ridge. Diductor scars large, flabellate, smooth or gently striated. Low marginal ridge may be developed around perimeter of ventral interior. Remainder of ventral visceral disc carries fine pustules and indistinct striations. Trail of valve smooth interiorly.

Fig. 1—A-Z, *Strophalosia irwinensis* Coleman. A-X, from Callytharra Formation, Carnarvon Basin; Y-Z, from Cuncudgerie Sandstone, Canning Basin. A-C, MUGD F6577, dorsal valve in ventral, dorsal and posterior views, $\times 2$, $\times 1.6$ and $\times 2.3$ respectively. D-E, MUGD F6581, dorsal valve in ventral and dorsal views, $\times 2$ and $\times 1.8$ respectively. F-G, MUGD F6582, shell in ventral and dorsal views, $\times 1.3$ and $\times 1.4$ respectively. H-K, MUGD F6578, shell in ventral, dorsal and posterior views, $\times 1.2$, enlargement of part of dorsal valve exterior, $\times 5.5$. L, MUGD F6583, shell in dorsal view, $\times 1.6$. M-N, MUGD F6584, shell in dorsal and ventral views, $\times 1.5$ and $\times 1.8$ respectively. O-P, MUGD F6585, shell in dorsal and ventral views, $\times 1.8$. Q-S, MUGD F6586, ventral valve in dorsal and posterior views, $\times 1.4$, enlargement of ventral interarea, $\times 3$. T-U, MUGD F6587, dorsal valve in dorsal and ventral views, $\times 1.8$ and $\times 2.2$. V, MUGD F6588, ventral valve internal mould, $\times 1.6$. W, MUGD F6589, shell in dorsal view, $\times 1.6$. X, MUGD F6580, dorsal valve in ventral view, $\times 2$. Y, CPC 24429, ventral valve internal mould, $\times 1.3$. Z, CPC 24430, ventral valve internal mould, $\times 1.6$.

Dorsal valve interior carries strong median septum; arises from cardinal process, extends some two-thirds of valve length. Adductor muscle scars smooth, in two pairs, with anterior pair most prominent. Muscle scars bisected by median septum. Cardinal process erect, inclined up to 60° to plane of visceral disc. Exteriorly cardinal process trilobed, in mature individuals, with central lobe being most prominent. Interiorly, cardinal process appears quadrilobed with large central lobe being gently bisected by gentle depression and a smaller lateral lobe occurring each side of central lobe. Anterior of interior of dorsal valve sharply turned into short trail.

Discussion: This species has been well described by Coleman (1957) and additional, large collections from the Callytharra Formation, upon which the above description was based, confirms the essential details of his description. *S. irwinensis* can now be confidently assigned to *Strophalosia* following the elucidation of the type species by Muir-Wood and Cooper (1960), Waterhouse (1964) and particularly Brunton (1966).

S. gerardi King (1846), from the Permian of the Himalayas, is a larger species than *S. irwinensis* and possesses prominent elongate dimples on the dorsal valve exterior and more numerous spines on the ventral valve (Brunton 1966, pl. 1, figs 8, 9). The umbonal shoulders of *S. gerardi* are much more prominent than those of *S. irwinensis*.

S. subcircularis Clarke (1970a) and its variants is a relatively large species with a cicatrix that may vary considerably in size (c.g. Clarke 1970a, pl. 1, fig. 6a) like that of *S. irwinensis*. The early Permian (Sakmarian) Tasmanian species is strongly convex with a variably-dimpled dorsal valve.

The Late Permian *S. diadema* (Waterhouse & Gupta 1983b) from the Southern Karakorum is a larger species with a shallow median sulcus but is only known from a few specimens and the illustrations of the species are not clear. Specimens attributed to *S. gerardi* by Waterhouse (1983, pl. 1, figs 1-2) from the Late Permian of Nepal are small and the dorsal exterior possesses irregular growth lamellae when compared with that of *S. irwinensis*. Comparison of *S. irwinensis* with *S. jimbaensis* sp. nov. is given under that species.

Both Prendergast (1943) and Coleman (1957) referred one imperfectly-preserved ventral valve from the Fossil Cliff Member to *Strophalosia tenuispina* Waagen (1884) but as noted by Coleman (1957, p. 131) the specimen could "equally as well belong to other species, in particular . . . *S. irwinensis*". The specimen is now formally referred to *S. irwinensis* in the interests of nomenclatural stability.

Strophalosia jimbaensis sp. nov.

Fig. 2A-G

HOLOTYPE: CPC 24405, a conjoined shell from the type section of the Jimba Jimba Calcareenite, Carnarvon Basin.

MATERIAL, LOCALITIES AND AGE: The four available specimens (all conjoined shells, 2 incomplete) are from the type section of the Jimba Jimba Calcareenite (Lat. 25°02'75"S; Long. 114°58'5"E), Jimba Jimba Station, 15 km west of Jimba Jimba Homestead (Condon 1967, p. 89), Carnarvon Basin. MUGD F6596-6598 come from 16.5 m above the base of the section. All specimens are Aklastian (Early Artinskian).

MEASUREMENTS (in mm): * = holotype, e = estimate

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height	Thickness	Height ventral interarea
CPC 24405*	18.7	37.2	31.8	28.0	8.2	1.8
MUGD F6596	20.0e	32.0c	27.5	24.6	—	2.4
MUGD F6597	23.0	38.0	26.5 +	23.5 +	10.7	2.8
MUGD F6598	19.2	34.6	—	—	11.5	2.0

DIAGNOSIS: Medium- to large-sized *Strophalosia*; moderately convex ventral valve; concave dorsal valve. Dorsal valve with well defined dimples, growth lamellae and radial capillae, no spines. Ventral valve with hinge spines, two rows on ears, numerous scattered sub-erect body spines and a shallow median sulcus.

DESCRIPTION: Shell medium- to large-sized, transversely oval in outline. Hinge width varies from about 0.5 of maximum width to 0.65 of maximum width (based on small collection). Hinge extremities rounded. Convexity of ventral valve relatively even judged from available specimens. Gentle median sulcus developed in ventral valve, persists until anterior margin of shell. Umbo small, weakly pointed; cicatrix small, extends from umbo for only a few mm. Dorsal valve gently concave at juvenile stages of ontogeny, becomes more distinctly concave in mature individuals. Ventral interarea prominent, flat, finely striated parallel to hinge line. Delthyrium small, high, narrow, filled with small, gently convex pseudodeltidium. Dorsal interarea distinct, relatively high; bisected by narrow, high, triangular notothyrium filled by gently convex chilidium.

Dorsal valve lacks spines but possesses prominent, concentric growth lamellae, low, fine, radial capillae between lamellae (about 3 per mm at 1.5 cm from umbo) and numerous scattered to subquincuncially arranged, circular to slightly elongate dimples (or pits).

Interior structure of the species not known.

Discussion: This species is described and named formally because of its larger size, shallow ventral sulcus and

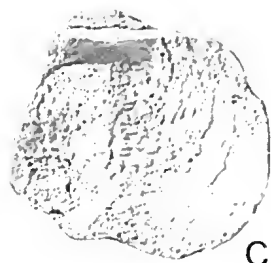
Fig. 2A-G—*Strophalosia jimbaensis* sp. nov. A-G, from Jimba Jimba Calcareenite, Carnarvon Basin. A-B, CPC 24405, holotype, shell in dorsal and ventral views, $\times 1.1$. C, MUGD F6596, crushed shell in dorsal view, $\times 1.2$. D-F, MUGD F6597, shell in dorsal, ventral and posterior views, $\times 1.1$. G, MUGD F6598, incomplete shell in dorsal view, $\times 1.2$. H-O, *Strophalosia* sp. cf. *S. jimbaensis* sp. nov., all from One Gum Formation, Carnarvon Basin. H, CPC 24431, natural cast of ventral valve in ventral view, $\times 1.2$. I, CPC 24435, natural cast of dorsal valve, interior view, $\times 1.2$. J, CPC 24433, natural cast of ventral valve in ventral view, $\times 1.2$. K, CPC 24434, natural cast of ventral valve in ventral view, $\times 1.2$. L, CPC 24432, natural cast of ventral valve in ventral view, $\times 1$. M, CPC 24436, natural cast of dorsal valve, interior view, $\times 1$. N, CPC 24437, natural cast of dorsal valve in dorsal view, $\times 1.2$. O, CPC 24438, natural cast of ventral valve, interior view, $\times 1.2$.



A



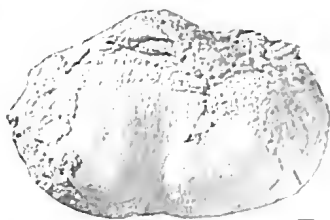
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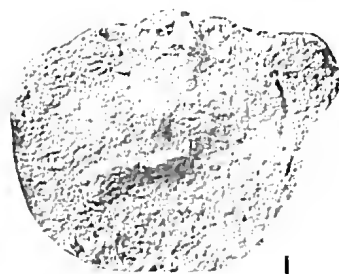
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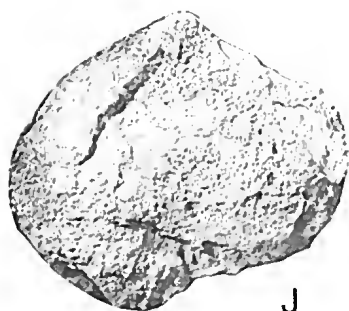
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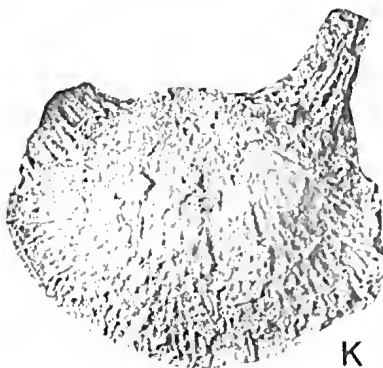
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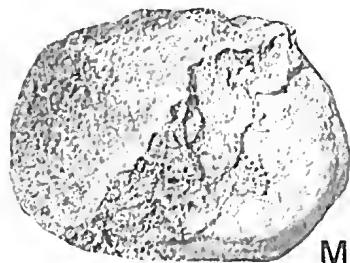
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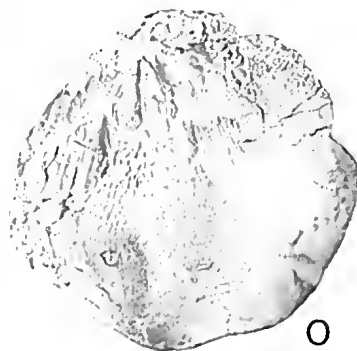
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O

strongly dimpled dorsal valve which collectively characterise a distinctive form. Nevertheless, further collections will add to the variation of the species and enable the elucidation of the internal structures.

S. jimbaensis sp. nov. is readily distinguished from *S. irwinensis* by means of the distinctive features of the species. *S. jimbaensis* sp. nov. is closer to both *S. gerardi* King and *S. subcircularis* Clarke in details of size, outline and spinosity but both the Himalayan and Tasmanian species appear to lack the distinctive shallow ventral sulcus and neither species possesses such well-developed dorsal valve dimples.

***Strophalosia* sp. cf. *S. jimbaensis* sp. nov.**

Fig. 2H-O

MATERIAL, LOCALITIES AND AGE: CPC 24431-24435, four natural casts (in ferruginous siltstone) of ventral valves and 1 natural cast of a dorsal valve from BMR locality WB 9, 2 km on a bearing of 285° from Keogh Hill, One Gum Formation. CPC 24436-24438, 2 natural casts of dorsal valves and 1 natural cast of a ventral valve (all in ferruginous siltstone) from BMR locality 78, 64, 042, 7, Glenburgh Run 13A, Photo 5009, 2.4 km at 276° from Keogh Hill, collector Dr J. M. Dickins, base of One Gum Formation. All Carnarvon Basin. All Akastinian (Early Artinskian).

MEASUREMENTS (in mm): Measurements are rounded off because preservation does not permit accuracy to one decimal place. e = estimate.

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height	Thickness
CPC 24431	—	38	32	—	9.0e
CPC 24433	—	35	35	—	11.0e
CPC 24434	—	39	33	—	—
CPC 24435	23	41	—	32	—
CPC 24437	21	39	—	29	—
CPC 24438	—	40+	38	—	—

DIAGNOSIS: Large *Strophalosia*. Ventral valve moderately convex with hinge spines, numerous scattered body spines and a shallow median sulcus. Dorsal valve concave with well-defined dimples, no spines.

DESCRIPTION: Shell large, transversely oval in outline. Convexity of ventral valve relatively even, no increase in convexity over visceral region. Gentle median sulcus developed in ventral valve, persists until anterior of shell. Dorsal valve gently concave.

Ornamentation of ventral valve consists of coarse scattered spines at times showing concentric and subquincuncial arrangement. Spine bases up to 1.0+ mm thick. Body spines semi-erect or recumbent—the better preserved specimens indicate they were primarily semi-erect. Numerous spines developed over small ears. Relationships of spines not clear but appears to be at least two rows present (spines spaced at 1-1.5 mm intervals adjacent to ears and at 2-3 mm intervals elsewhere on valve).

Dorsal valve lacks spines but possesses prominent concentric growth lamellae and distinct, circular to slightly elongate dimples.

Ventral valve interior carries smooth adductor scars, posteriorly located, bisected by low ridge. Diductor scars less well impressed, appear large, flabellate, striate.

Dorsal valve interior with distinct median septum, arising from cardinal process (details unknown). Low to prominent marginal ridge present. Brachial ridges poorly known.

DISCUSSION: The specimens discussed are closest to *S. jimbaensis* sp. nov. in details of ventral valve morphology and dorsal valve exterior ornament but information on the nature of the cardinal area of the One Gum Formation specimens and the internal morphology of *S. jimbaensis* sp. nov. is required for a confident referral of the material at hand to that species. Nevertheless the two occurrences appear to be closely related. The present material is distinct from other species of *Strophalosia* on similar grounds to those discussed for *S. jimbaensis*.

Genus *Heteralosia* King, 1938

TYPE SPECIES: *Heteralosia slocomi* King, 1938.

DIAGNOSIS: Small *Strophalosiinae* with erect and recumbent spines over ventral valve. Dorsal valve with no spines but with concentric lamellae, usually non-capillate. Delthyrium filled by dorsal cardinal process when valves closed and/or narrow pseudodeltidium. Outline of shell rounded, usually with small ears. Brachial ridges often weakly developed.

DISCUSSION: As noted by Clarke (1970a, p. 21), although the original diagnosis of *Heteralosia* was based on a false premise (that the type species of *Strophalosia* was a species with a spinose dorsal valve) there appears to be good evidence for the validity of the genus. Nevertheless the genus is close to *Strophalosia* s.s. and it can be noted that King (1938) placed *Strophalosia gerardi* in his genus. It would appear that many species of *Heteralosia* spent most if not their entire life permanently attached to a supporting object. Species of *Strophalosia* were apparently well detached by maturity. However, size of the cicatrix is not a guide to a particular species duration of attachment. The largest specimen of *Strophalosia irwinensis* described herein happens to possess the largest cicatrix of any specimen of the species seen by the author but that species shows a wide variation in cicatrix size. Coleman used the size of the cicatrix as one of his criteria for recognition of species within *Heteralosia* and hence not surprisingly, species of the genus appeared to range throughout almost the entire Permian sequence of Western Australia. Clarke (1970a) considered that *Heteralosia* was characterised by weak brachial ridges as did Grant (1976). However, illustrations of various species of *Heteralosia* from the Glass Mountains provided by Cooper and Grant (1975) reveal many individuals with well-developed brachial ridges. Some specimens of *H. etheridgei* described herein also possess clearly-developed brachial ridges.

Waterhouse (1959, 1964, 1969, 1981) has repeatedly drawn attention to the need for a consideration of the ontogeny of strophalosiid shells when describing strophalosiid species. As a result he and Brunton (1966)

have queried the validity of *Heteralosia*. Nevertheless, the observation that some specimens of species such as *H. etheridgei* possess well-developed brachial ridges (which the present author considers to be a feature of adult or, at least, submature shells) leads to the conclusion that two groups of strophalosiids with non-spinose dorsal valves occur in the Western Australian Permian faunas. Attempts have been made herein to discriminate between juvenile *Strophalosia irwinensis* and mature *Heteralosia etheridgei*. As a result the present author agrees with Clarke (1970a) and Grant (1976) that *Heteralosia* is a useful generic concept. However, Waterhouse (1959) has clearly established the importance of ontogenetic studies in the group.

Both Prendergast (1943) and Coleman (1957) confused the productacean genus *Etheridgina* Oehlert with small attached strophalosiids. The productacean characters of *Etheridgina*, well shown by Etheridge (1876, 1878) and Oehlert (1887) were confirmed by the modern studies of Waterhouse (1959) and Muir-Wood and Cooper (1960). Prendergast (1943) and Coleman (1957) were apparently confused by Etheridge's (1918) use of the trivial name *complectens* for his new species of *Strophalosia*. Etheridge, of course, did not refer to his previous use of the trivial name *complectens* for his "*Productus*" (i.e. *Etheridgina*) as the two species were not related. The suppression of the binomen *Strophalosia complectens* by both Prendergast and Coleman is not justified and hence the name is restored herein. Greger's (1920) erroneous treatment of *Etheridgina* undoubtedly added to the confusion for subsequent authors. Prendergast (1943, p. 53) appears to have examined and misinterpreted specimens of *Etheridgina* from Scotland.

***Heteralosia etheridgei* (Prendergast, 1943)**

Fig. 3A-Z, AA-BB

1943 *Strophalosia* cf. *Strophalosia beecheri*: Prendergast, p. 41, pl. 5, figs 1-3.

1943 *Strophalosia etheridgei* Prendergast, p. 43, pl. 5, figs 5-12.

1943 *Strophalosia* sp. ind. A. Prendergast, p. 51, pl. 6, figs 10-12.

1957 *Strophalosia (Heteralosia) etheridgei* Prendergast, Coleman, p. 120, pl. 19, figs 30-32.

1957 *Strophalosia (Heteralosia) prendergastae* Coleman (partim.), p. 127, pl. 20, figs 25-28 (non cct.).

LECTOTYPE: GSWA 1/5252a, figured by Prendergast (1943, pl. 5, figs 6, 7) from creek 0.8 km (0.5 mile) west of Callytharra Springs, Wooramel River, Carnarvon Basin. Callytharra Formation. Chosen by Coleman (1957, p. 120).

MATERIAL, LOCALITIES AND AGE: Specimens as figured and measured in addition to abundant material from the Callytharra Formation, collected by Dr G. A. Thomas, University of Melbourne. MUGD F6599-6602, 4 isolated dorsal valves from G. A. Thomas locality Q545, from measured section on a creek near Gap Pool, Wooramel River, 4.6 km bearing 333° from Keogh Hill, Wooramel River district, 42.5-46 m above base of section, Callytharra Formation. MUGD F6603, 1 isolated

ventral valve from G. A. Thomas locality Q550, same section as above, 56 m above base of section. MUGD F6604, 1 isolated ventral valve from G. A. Thomas locality Q556, same section as above, 42.5-57 m above base of section. MUGD F6605, 1 isolated ventral valve from G. A. Thomas locality Q559, same section as above, 76 m above base of section. MUGD F6606, 6607, 1 isolated dorsal valve and 1 conjoined shell from G. A. Thomas locality P498, type section of Callytharra Formation, Callytharra Springs, 34-38 m above base of section. MUGD F6579, 1 isolated dorsal valve from G. A. Thomas locality P495, same section as above, 33 m above base of section. CPC 24406, 24439, 24440, 3 conjoined shells from BMR locality GW87, type section of Callytharra Formation, Callytharra Springs, 10-17 m above base of section. All Carnarvon Basin.

GSWA F270, external mould of dorsal valve from Fossil Cliff, Irvin River District, Perth Basin, Fossil Cliff Member of the Holmwood Shale. A ventral valve from the Fossil Cliff Member was figured by Coleman (1957; pl. 19, figs 27-28).

All Sterlitamakian (Late Sakmarian).

SIZE RANGES: A total of 22 specimens (including the figured specimens) were measured. Hinge width, 3.3-9.5 mm; maximum width, 4.6-12.9 mm; ventral valve height, 5.0-13.0 mm; dorsal valve height, 4.0-10.8 mm; thickness, 2.0-6.2 mm; ventral interarea height, 0.5-1.4 mm; dorsal interarea height, 0.2-1.2 mm.

DIAGNOSIS: Small *Heteralosia*; elongate to circular outline. Cicatrix often small, in a few specimens relatively large. Exterior ornament of pronounced concentric lamellae and widely spaced, usually relatively coarse, ventral spines. Dorsal exterior with fine capillae and scattered, widely-spaced dimples.

DESCRIPTION: Shell small, elongate oval to circular in outline. Hinge width varies from two-thirds to over seven-eighths maximum width. Hinge extremities usually finely pointed in mature specimens. Small ears, poorly demarcated from rest of shell, may be developed. Juvenile specimens with hinge extremities more rounded. Ventral valve strongly convex with convexity decreasing anteriorly. Maximum width at about mid-length of shell. Umbo invariably flattened, carries distinct cicatrix of attachment, usually small in size, but, in a few specimens, attaining relatively large size (the two largest measured: Specimen MUGD F6605, 6 mm wide, 4 mm long; Specimen MUGD F6607, 5 mm wide, 3.5 mm long). Ornamentation of ventral valve consists of spines and concentric lamellae. Spines distributed as row along hinge, when cicatrix small, and moderately to widely spread along concentric rows over valve. Spines may be spaced at intervals of 3 mm or more, in which case specimen may have relatively few spines (e.g. Specimen CPC 24406 has some 27 spines), or at about 2 mm intervals. Spines relatively coarse (e.g. up to 0.6 mm thick on specimen CPC 24440), tend to be adherent posteriorly, suberect anteriorly.

Interareas distinct, flat, extend full width of hinge, relatively low. Ventral interarea striated parallel to hinge, bisected by narrow triangular delthyrium filled by



weakly-convex pseudodeltidium. Dorsal interarea about half to two-thirds height of ventral interarea, weakly striate parallel to hinge line, bisected by triangular, flat to weakly-convex, chilidium.

Dorsal valve flat or gently convex during earliest stages of ontogeny, then becomes increasingly concave anteriorly and tends to be distinctly geniculated in front of visceral disc. Concentric lamellae distinct exteriorly; when well preserved may carry fine capillae (some 3 to 4 per mm on Specimen CPC 24406). Spines absent.

Ventral teeth small, divergent. Marginal ridge, arising near teeth may continue laterally, demarcating small ears clearly, then die out on lateral margins of valve. Adductor scars situated high up under umbo on small raised platform; diductor scars poorly impressed, weakly striate. Anterior of interior of ventral valve smooth.

Cardinal process arises from strong median septum and two, small lateral ridges which surround small, deep sockets. Process spike-like, extending posteriorly at small angle to plane of dorsal interarea; its interior face bilobed in juvenile specimens (because of a pronounced groove bisecting the single, large lobe), quadrilobed in mature specimens with small lateral lobes becoming developed.

Smooth dorsal adductor scars distinct, particularly in mature specimens; often raised above level of visceral disc; bisected by median septum, not differentiated into anterior and posterior components. Median septum usually slightly more than half valve length, raised anteriorly. Abundant papillae occur around anterior of valve. Brachial ridges variably developed but some specimens show distinct, typical, strophalosiid brachial ridges.

DISCUSSION: Specimens at hand modify the understanding of this species from that given by Prendergast (1943) and Coleman (1957). The cicatrix of attachment may vary considerably in size and this, in turn, may impart a distorted outline to some specimens. For these reasons a Callytharra specimen previously referred to *H. prendergastae* by Coleman (1957) is now referred to *H. etheridgei*, as discussed under *H. prendergastae*. Spinosity varies more than allowed for by Coleman (1957) although ventral spines are apparently never as dense as those of *H. prendergastae*. One specimen (MUGD F6604) possesses the typical spine pattern of the

species but is unusual in that the spines are fine (only being 0.3 to 0.4 mm wide); it is presumed to be a variant of the species.

H. etheridgei is close to *H. prendergastae* but is differentiated from that species by a less densely spinose ventral valve and a dorsal valve with well developed concentric lamellae and only rarely with dimples. On average *H. etheridgei* is a smaller species than *H. prendergastae*.

Juveniles of *Strophalosia irwinensis* are close to *H. etheridgei* but invariably possess a less-convex ventral valve (at comparable sizes) and often have a larger flat cicatrix of attachment. Juveniles of *S. irwinensis* also tend to be more transverse in outline than *H. etheridgei* and to have more closely-spaced, finer, ventral spines. Juvenile *S. irwinensis* are measured and figured in a discussion of that species.

The *Strophalosia rarispina* of Mansuy (1914) from Phnom Ta Maol, Cambodia (Mansuy 1914, pl. 2, figs 9a-d) has a strongly-developed ventral convexity, small umbonal cicatrix and elongate outline that recall *H. etheridgei* but the Cambodian shell has a very low ventral interarea.

H. haerens Grant (1976, p. 83, pl. 18, figs 1-28) is also moderately close to *H. etheridgei* but is distinguished from the Western Australian species by its normally larger cicatrix of attachment and lack of pseudodeltidium. The Thailand species, from the Late Early Permian, is also much smaller than *H. etheridgei*.

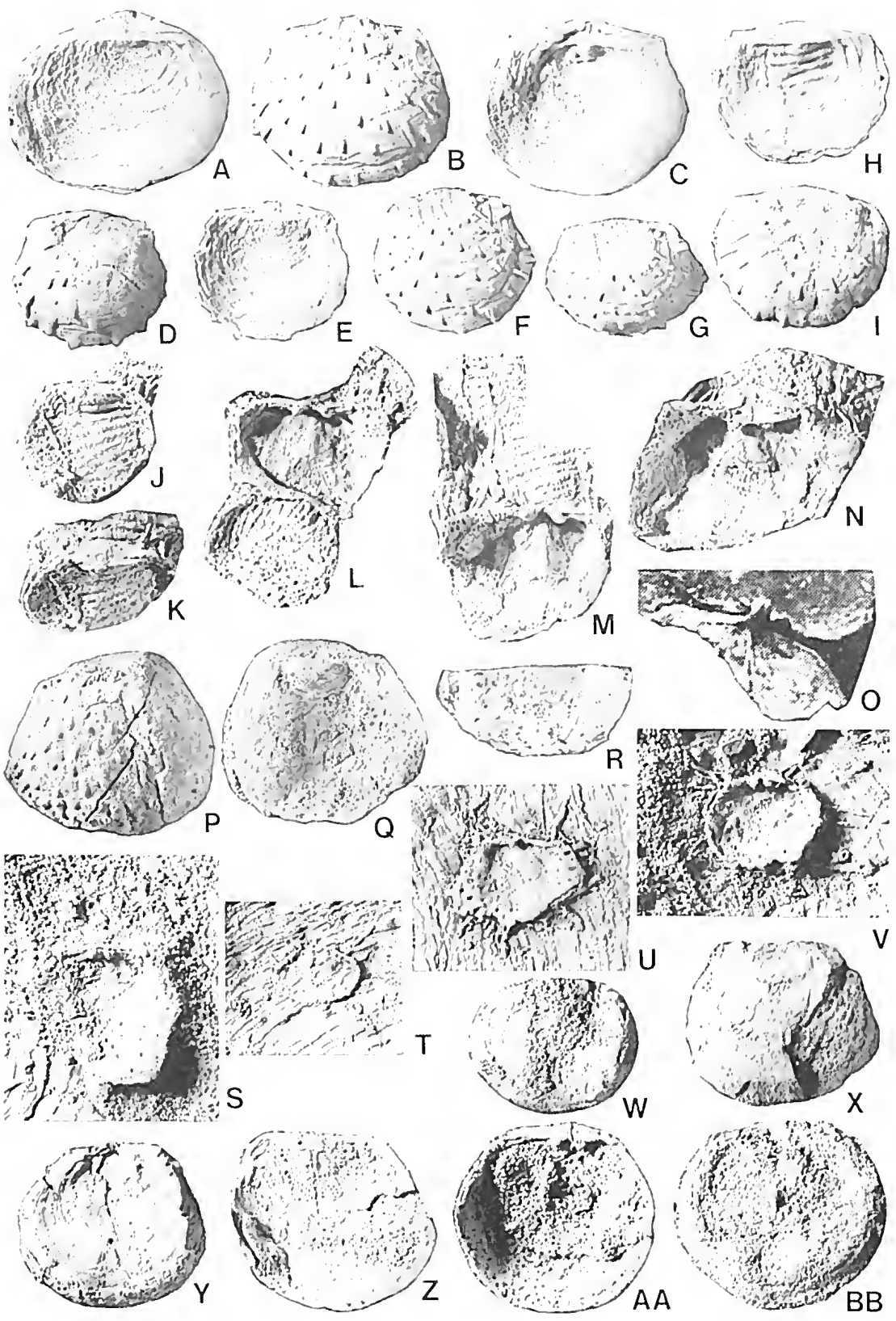
Heteralosia prendergastae (Coleman, 1957)

Fig. 4P-R

1957 *Strophalosia* (*Heteralosia*) *prendergastae* (Coleman (partim.), p. 127; pl. 20, figs 20-24 (non cet.) HOLOTYPE: UWA 28444a, a conjoined shell from the Cundlego Formation, Carnarvon Basin.

MATERIAL, LOCALITY AND AGE: Only the holotype of the species is known; the paratype (UWA 28444b) cannot be located in the UWA collections. The type locality is: 350 yards (approx. 320 metres) west of fence between Barabiddy and Weer Paddocks, 2220 yards (approx. 2 km) south of gate in that fence, near Barabiddy Creek, south of Wandagee Homestead, Carnarvon Basin, Cundlego Formation. Late Baigendzhinian (Late Artinskian).

Fig. 3—A-Z, AA-BB, *Heteralosia etheridgei* (Prendergast). A-Z, AA, from Callytharra Formation, Carnarvon Basin; BB, from Fossil Cliff Member, Perth Basin. A-B, MUGD F6599, dorsal valve in ventral and dorsal views, $\times 3.5$. C-D, MUGD F6600, dorsal valve in ventral and dorsal views, $\times 3.5$. E-F, MUGD F6601, dorsal valve in ventral and dorsal views, $\times 4$. G-H, MUGD F6606, dorsal valve in ventral and dorsal views, $\times 4$ and $\times 3.5$ respectively. I, MUGD F6604, ventral valve in ventral view, $\times 2.6$. J, MUGD F6579, dorsal valve in ventral view, $\times 4.5$. K-M, CPC 24406, shell in posterior, dorsal and ventral views, $\times 3.5$, $\times 3$ and $\times 3.5$ respectively. N-P, MUGD F6607, shell in dorsal, ventral and posterior views, $\times 3.2$, $\times 3.8$ and $\times 3.8$ respectively. Q-R, MUGD F6603, ventral valve in ventral and dorsal views, $\times 4.5$ and $\times 3.8$ respectively. S-T, CPC 24439, shell in ventral and dorsal views, $\times 4.5$ and $\times 3$ respectively. U-W, CPC 24440, shell in ventral, posterior and dorsal views, $\times 4$, $\times 4$ and $\times 3$ respectively. X-Y, MUGD F6605, ventral valve in ventral and dorsal views, $\times 3.5$. Z, AA, MUGD F6602, dorsal valve in ventral and dorsal views, $\times 3.6$. BB, GSWA F270, external mould of dorsal valve, $\times 3.5$.



MEASUREMENTS (in mm): Measurements of the paratype are from Coleman (1957). * = holotype.

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height	Thick-ness	Height ventral interarea
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UWA 28444a*	7.5	12.5	1.5	10.3	4	1.1
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UWA 28444b	7.5	13.5	15.7	—	5	—
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DIAGNOSIS: Small *Heteralosia*, not attached as adults, with numerous fine ventral spines and irregularly dimpled dorsal exterior. Cicatrix prominent.

DESCRIPTION: Shell small with subcircular outline. Cicatrix distinct, may distort outline posteriorly. Cicatrix flat, arises on umbo, hence umbo not clearly demarcated. Anterior of cicatrix, ventral valve evenly, strongly convex. Transversely, lateral slopes steep; middle of ventral valve less convex, no sulcus present. Hinge line straight, about 0.6 of maximum shell width. Maximum shell width at mid length of shell. No distinct cars present. Ventral interarea low, bisected by narrow, triangular delthyrium filled with slightly-convex pseudo-deltidium.

No spines on cicatrix. Remainder of ventral valve covered with numerous fine, spine bases, often elongated, that give rise to recumbent or semi-erect spines. Spine bases fine, none exceed 0.5 mm in width; arranged in semiquincuncial manner. No growth lamellae on ventral valve.

Dorsal valve moderately concave. Initial part of valve flat; anteriorly, valve becomes evenly concave, flattening towards anterior margin. Dorsal interarea low, bisected by small, distinct chlidium. Valve exterior aspinose, growth lines poorly developed. Valve exterior carries numerous, randomly scattered dimples.

Interior of shell unknown.

DISCUSSION: This species is one of the least well-known strophalosiid species from the Western Australian Permian. Coleman (1957) indicated a wide stratigraphic range for the species (Sterlitamakian to Chhidruan as used herein) and this requires substantial reappraisal. Several of his specimens were from the Hardman Formation of the Canning Basin. These (Coleman 1957, pl. 20 figs 29-35) can confidently be assigned to *Echinosia* (*Notosia*) *dickinsi* subgen. et. sp. nov. described below; they have been well figured by Coleman and are characteristic of the new subgenus and species. *H. prendergastae* was also recorded by Coleman (1957, pl.

20, figs 25-28) from the Callytharra Formation. The Callytharra specimen is referred by mc to *H. etheridgei* Prendergast; it is partly decorticated and hence does not clearly display the coarser, more numerous spines of the holotype of *H. prendergastae* and it also possesses more well-developed dorsal growth lamellae as in *H. etheridgei*. Coleman (1957) categorised his species by its more numerous, fine spines (but coarser than those of *H. etheridgei*), larger size, more quadrate outline and large cicatrix of attachment. However, new collections of *H. etheridgei* show that the species can be larger than previously realised and that the cicatrix of attachment varies in size for the species (although it does not often appear to be as large as that of the holotype of *H. prendergastae*). Difficulties of distinguishing between *H. etheridgei* and juveniles of *Strophalosia irwinensis* are discussed under *H. etheridgei* but Coleman's Callytharra specimen is more circular to elongate and strongly ventrally convex than is normal for juvenile *S. irwinensis*. The revision of *H. etheridgei* given above indicates that *H. prendergastae* is better characterised by its more numerous ventral spines and a dorsal exterior with no distinct growth lamellae and an irregularly dimpled surface. Nevertheless large collections from the Cundlego, and possibly Wandagee Formations are required to place the species on a firm understanding.

H. prendergastae is probably closely related to *H. iphia* Grant (1976, p. 84, pl. 18, figs 29-50) from the Late Early Permian of Thailand. Grant's species possesses numerous ventral spines, a distinct cicatrix and a dorsal exterior with irregularly-scattered dimples and variably-developed growth lamellae.

Heteralosia compectens (Etheridge, 1918)

Fig. 4J-O

- 1915 *Strophalosia* sp. Etheridge, p. 34; pl. 5, figs 16-18
- 1918 *Strophalosia compectens* Etheridge, p. 253; pl. 40, figs 11-12
- 1926 *Strophalosia compectens* Etheridge; Glauert, p. 46
- 1943 *Etheridgina muirwoodae* Prendergast, p. 54; pl. 6, figs 14, 15
- 1957 *Etheridgina*(?) *muirwoodae* Prendergast; Coleman, p. 109; pl. 17, figs 6-11
- 1958 *Etheridgina*(?) *muirwoodae* Prendergast; Guppy et al., p. 48

Fig. 4—A-I, *Strophalosia irwinensis* Coleman. A-I, from Callytharra Formation, Carnarvon Basin. A, MUGD F6591, shell in dorsal view, $\times 3$. B-C, MUGD F6592, shell in ventral and dorsal views, $\times 3$. D-E, MUGD F6593, shell in ventral and dorsal views, $\times 3.6$. F-G, MUGD F6594, ventral valve in ventral and posterior views, $\times 3$. H-I, MUGD F6595, shell in dorsal and ventral views, $\times 3$. J-O, *Heteralosia compectens* (Etheridge). All from Noonkanbah Formation, Canning Basin. J-K, AMF16699a, lectotype, shell in dorsal and posterior views, $\times 3$. L, AMF16812, ventral valve and incomplete shell in dorsal views, $\times 3$. M, AMF16699b, ventral valve in ventral view, $\times 2.6$. N, AMF16699c, ventral valve in ventral view, $\times 2.6$. O, missing dorsal valve, copy of figure from Etheridge (1918, pl. 40, fig. 11) $\times 3.5$. P-R, *Heteralosia prendergastae* (Coleman), from Cundlego Formation, Carnarvon Basin, holotype, UWA 28444a, shell in ventral, dorsal and posterior views, $\times 3$. S-V, *Heteralosia* sp. A, all from Madeline Formation, Carnarvon Basin. S, CPC 24441, ventral valve in dorsal view, $\times 2.8$. T, CPC 24444, ventral valve in dorsal view, $\times 3$. U, CPC 24442, ventral valve in dorsal view, $\times 3$. V, CPC 24443, ventral valve in dorsal view, $\times 3$. W-Z, AA-BB, *Heteralosia* sp. B, all from Lightjack Formation, Canning Basin. W, CPC 24450, dorsal valve in ventral view, $\times 2.5$. X, CPC 24448, dorsal valve in ventral view, $\times 2.5$. Y, CPC 24449, dorsal valve in ventral view, $\times 2.5$. Z, CPC 24447, dorsal valve in dorsal view, $\times 2.5$. AA, CPC 24445, ventral valve in dorsal view, $\times 2.5$. BB, CPC 24446, dorsal valve in ventral view, $\times 2.5$.

1967 *Etheridgina muirwoodae* Prendergast; Condon, p. 169

LECTOTYPE: Entire specimen on AMF 16699 (designated herein as AMF 16699a), chosen by Coleman (1957, p. 109), from Mount Marmion, West Kimberley District; Noonkanbah Formation.

MATERIAL, LOCALITY AND AGE: The syntypic series described by Etheridge (1918) was reexamined. The incomplete dorsal valve figured by Etheridge (1918, pl. 40, fig. 11) has been lost—the specimen was not available to either Prendergast (1943) or Coleman (1957). The syntypic series and specimens previously available to Etheridge (Etheridge, 1915) came from Mt Marmion, West Kimberley District, Canning Basin (see also Glauert, 1926), now included in the upper part of the Noonkanbah Formation. Coleman (1957) also recorded and figured specimens from several localities from the Wandagee Formation, Carnarvon Basin. They were well described and figured (Coleman, 1957, p. 110, pl. 17, figs 6, 10, 11) and are conspecific with the Mount Marmion material. Measurements of the species are provided by Coleman (1957, p. 110). Late Baigendzhinian (Late Artinskian).

DIAGNOSIS: Small *Heteralosia*, adherent by most of ventral valve and by coarse, long, adherent, ventral spines. Well-developed interareas, teeth, elevated, internally-bilobed cardinal process and dorsal median septum.

DESCRIPTION: Shell small, subquadrate to transversely oval in outline. Hinge width varies from just over half maximum width up to seven-eighths maximum width. Hinge extremities become pointed in mature samples, with suggestion of small ears being developed, rounded in submature, younger specimens. Ventral valve firmly fixed to underlying substrate (in all known samples, a larger brachiopod) with entire visceral disc being attached. Lateral and anterior margins of ventral valve free, being sharply upturned, not attached. Ornamentation of ventral valve consists of spines distributed along cardinal, lateral and anterior margins; number of spines variable. Spines relatively coarse, adherent to host shell, longer than shell on some specimens.

Interareas prominent, flat, extend full width of hinge; also relatively high. Ventral interarea may vary between being perpendicular to, or parallel to, plane of attachment, variation being caused by degree to which umbo itself is attached to substrate. Umbo minute, barely noticeable. Ventral interarea bisected by relatively-wide delthyrium filled by pseudodeltidium which is only slightly raised above level of interarea. Dorsal interarea half height of that of ventral interarea, flat to gently concave; bisected by notothyrium filled by triangular chilidium. Both interareas lie in one plane.

Ventral valve teeth usually strong, divergent. Diductor muscle scars large, smooth, lobate, bisected by low ridge or median septum. Adductor scars poorly differentiated. Anterior or interior of ventral valve finely pustulose, posterior cardinal margins carry numerous pits arranged in two, ill-defined rows.

Dorsal valve thin, gently concave to flat. Fine growth lamellae may be present. Valve may reflect exteriorly ornament of substrate shell—the lectotype reflects orna-

ment of ribs of piece of *Neospirifer* sp. which acts as substrate of specimen. Dorsal valve without spines. Cardinal process prominent, exteriorly trilobed (*vide* Prendergast 1943), interiorly bilobed; inclined at almost right angle to dorsal interarea. Median septum short, fine, extends from base of process; bisects muscle field (Prendergast 1943) or, apparently, weakly dendritic (Etheridge 1918, pl. 40, fig. 11). Brachial ridges unknown.

DISCUSSION: The above description is based on a reexamination of Etheridge's (1918) syntypic series of *H. complectens* and, particularly for details of the dorsal valve, descriptions of the species by Prendergast (1943) and Coleman (1957) as well as Etheridge's (1918) illustration of the now missing syntypic dorsal valve. Etheridge's (1918) name for the species was suppressed by both Prendergast (1943) and Coleman (1957) who both mistakenly confused this small strophalosiid with *Etheridgina*, a productidiniid. The fact that Etheridge (1918) used the same trivial name, *complectens*, for his adherent strophalosiid as he had used for his adherent productidiniid some 50 years previously (Etheridge 1876, 1878) appears to have added to the confusion but Etheridge (1918) presumably did not refer to his adherent productidiniid as he considered the two were not closely related. Etheridge's (1918) specific name *Strophalosia* (now *Heteralosia*) *complectens* is restored and its clear strophalosiid affinity is indicated, as shown by Etheridge and implied by Prendergast (1943) and Coleman (1957) and also indicated by Clarke (1970a) and Grant (1976). Waterhouse (1959) and Muir-Wood and Cooper (1960) reconfirmed the productidiniid relationship of *Etheridgina* as shown by Etheridge (1876, 1878).

Heteralosia complectens is readily distinguished from other West Australian species of the genus by its smaller size, largely-adherent ventral valve and long, adherent, ventral spines. The substantial area of the ventral valve that is adherent and the long adherent spines also readily distinguish the species from the small *H. haerens* Grant (1976) from limestones of approximately similar age from Southern Thailand. *H. hystricula* Girty as figured by Cooper and Grant (1975, pl. 195) is a larger species than *H. complectens* with finer spines, less-adherent ventral valve and lower interareas; it comes from the Late Wordian and Roadian of Texas. *H. magnispina* Cooper and Grant (1975) from the Kazanian of Texas has much lower interareas than *H. complectens* but is also strongly adherent. The two Texan species are probably convergent with *H. complectens* in terms of their adherent ventral valves.

Heteralosia sp. A

Fig. 4S-V

MATERIAL, LOCALITY AND AGE: CPC 24441-24444, four small ventral valves attached to the dorsal valve of *Wyndhamia* sp. nov. specimen from BMR locality WB11, 2.4 km on a bearing of 143° from Mount Madeline, upper part of Madeline Formation, Carnarvon Basin. Early Baigendzhinian (Late Artinskian).

MEASUREMENTS (in mm): e = estimate

Specimen	Maximum width	Hinge width	Ventral height
CPC 24441	9.6	7.1	8.0
CPC 24442	7.6	4.8e	5.5 +
CPC 24443	6.4	4.3e	5.5
CPC 24444	4.8	—	3.9

COMMENTS: The four small ventral valves, adherent to the host shell for much of their valves by means of long, fine adherent spines indicate a species close to *Heteralosis complectens* (Etheridge, 1918). Differences from that species are indicated by the fineness of the adherent spines and the low ventral interarea with a small, inconspicuous delthyrium and pseudodeltidium on even the largest specimen.

There is always a possibility that poorly known, small species referred to *Heteralosis* may simply be juvenile spats of large strophalosiid species (Waterhouse, 1981, p. 67) but, for the present, the four specimens appear to represent a distinctive adherent species of *Heteralosis*.

***Heteralosis* sp. B**
Fig. 4W-Z, AA-BB

1907 *Strophalosia* sp. Etheridge, p. 7, pl. 6, fig. 8; pl. 7, figs 2-4

1958 *Strophalosia* (*Heteralosis*) *prendergastae*: Guppy *et al.*, p. 53

1958 *Etheridgina muirwoodae*: Guppy *et al.*, p. 53.

MATERIAL, LOCALITY AND AGE: CPC 24445-24450, one incomplete ventral valve and five incomplete dorsal valves from BMR locality CR 1133, Lat. 19°09'51"S, Long. 125°59'57"E, Lightjack Formation, Canning Basin. Middle Kungurian.

MEASUREMENTS (in mm):

Specimen	Maximum width	Hinge width	Ventral height	Dorsal height
CPC 24445	13.9	6.6	13.4	—
CPC 24446	15.5	10.6	—	13.4
CPC 24447	13.8	6.7	—	11.8
CPC 24448	12.8	8.2	—	11.2
CPC 24449	12.4	6.8	—	11.8
CPC 24450	12.6	7.8	—	10.7

COMMENTS: The specimens, all of variable preservation, indicate a large species of *Heteralosis* that was attached only during its early ontogenetic stages. The ventral valve carries numerous fine spines that were erect anteriorly (judging from the spine bases). The ventral interarea is distinct and carries a narrow triangular delthyrium filled with a poorly-known pseudodeltidium. The ventral valve is strongly convex. The dorsal valve is weakly convex posteriorly, flattish medianly and strongly concave and geniculate anteriorly. The median septum is half the length of the valve, sharp, thin and arises at the base of an erect, blunt, weakly-bilobed cardinal process. An internal marginal ridge is developed anteriorly preceding the pronounced geniculation of the valve.

The material can be compared with the poorly-known *Strophalosia* sp. of Etheridge (1907, pl. 6, fig. 8;

pl. 7, figs 2-4) from correlatable strata (the Lower Marine Beds of the Port Keats Group) in the Bonaparte Gulf Basin. Etheridge's specimens have not been located; they are not in the South Australian Museum which houses many other specimens of his 1907 work. The illustrations provided by Etheridge indicate a species with a circular outline, finely-spinose ventral valve and a dorsal valve with a fine, sharp, median septum and an anteriorly-developed marginal ridge. Etheridge's (1907) *Strophalosia* sp. is therefore included within my *Heteralosis* sp. B.

Comparison with other Western Australian species of *Heteralosis* is hampered by the poor preservation of the material but *Heteralosis* sp. B is apparently the species indicated by Guppy *et al.* (1958) in the two citations in the synonymy quoted above.

Genus *Echinalosis* Waterhouse, 1967

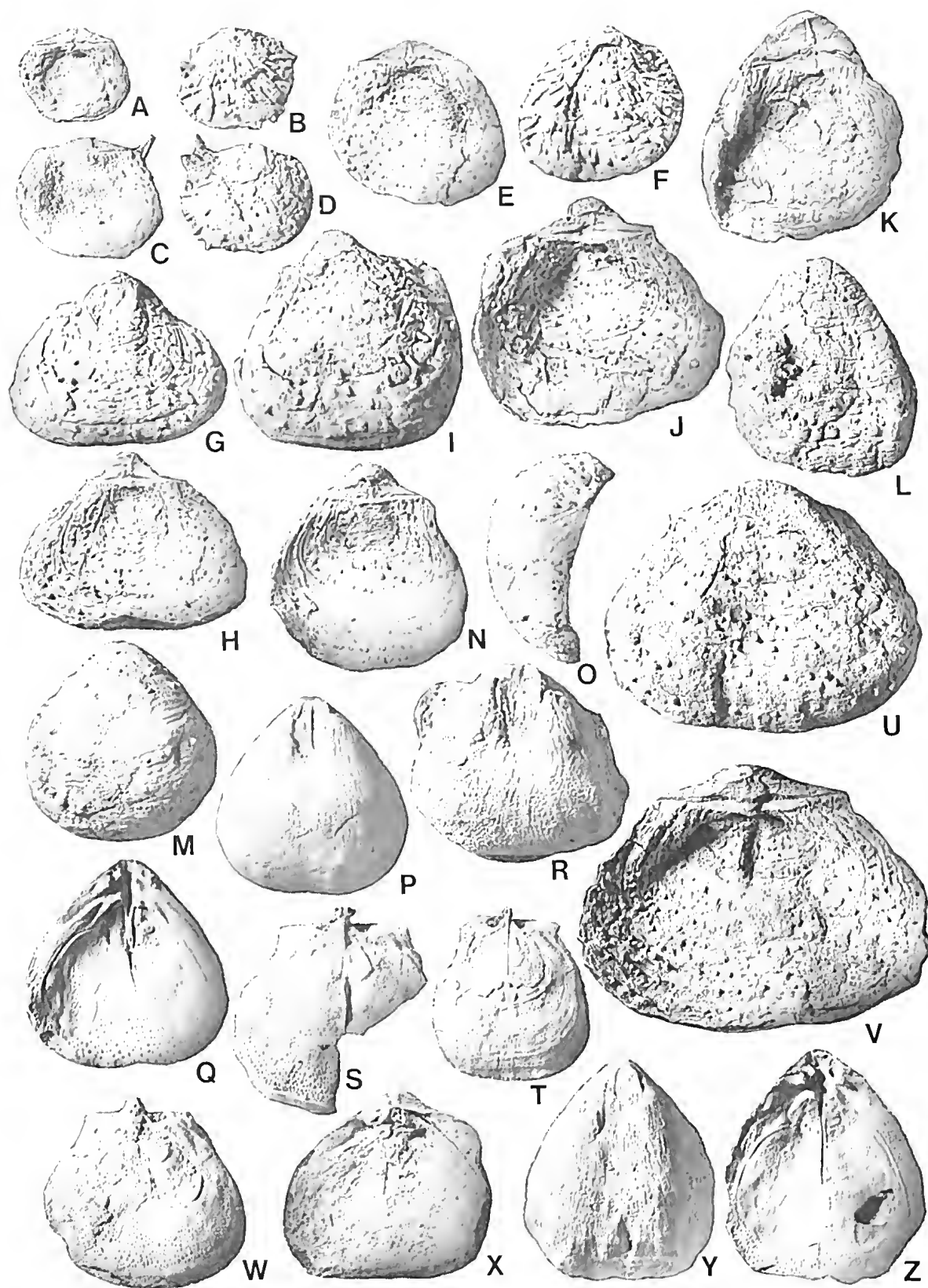
= *Multispinula* Waterhouse, 1966, *non* Rowell, 1962

TYPE SPECIES: *Strophalosia maxwelli* Waterhouse, 1964.

DIAGNOSIS: Concave-convex strophalosiids, circular to elongate in outline. Dorsal valve with trail not thickened. Ventral spines erect and semi-recumbent; dorsal spines finer than ventral spines and erect (modified from Waterhouse 1969, p. 29).

DISCUSSION: This genus is usefully separated from *Wyndhamia* Booker (1929) by details of shell outline and the dorsal valve. Two strophalosiid species from Western Australia belong in *Echinalosis*. Clarke (1970a, p. 20 and p. 21) considered that *Strophalosia prideri* Coleman might be an *Orthothrix*. *Orthothrix* Geinitz (1847a, 1847b) lapsed until reestablished by Muir-Wood and Cooper (1960) and is restricted to small strophalosiids with a trigonal posterior outline to the shell, fine, long, recumbent spines on the ventral valve and minute spines on the dorsal valve. Waterhouse (1969) referred *Strophalosia prideri* to *Echinalosis* and that assignment is followed herein. Nevertheless, the dorsal spines of *Strophalosia prideri* are much coarser than those of *Strophalosia maxwelli* Waterhouse (1964) as noted by Clarke (1970a). The genus morphologically closest to *Echinalosis* is *Marginalosis* Waterhouse (1978a, p. 64) with ?*Echinalosis kalikotei* Waterhouse (1975) as type species. *Marginalosis* possesses erect spines on the ventral valve (finer than on *Echinalosis*) and a thick marginal ridge on the interior of both valves (see Waterhouse 1978a, for full discussion).

DISTRIBUTION: *Echinalosis* is abundant in the Permian faunas of New Zealand and Eastern Australia (Waterhouse 1966, 1969, Dear 1971, Clarke & Farmer 1976), present in the Permian of Western Australia and present in the Himalayas (Waterhouse 1966, Chang & Ching 1976) and probably the Salt Range (as discussed by Waterhouse, 1966). The genus has been described from Arctic Canada (Waterhouse, 1969) and is possibly present in north-eastern Siberia in the form *Strophalosia? bajkurica* Ustritskiy as summarised and referred to *Strophalosia* by Grigor'eva (1977). *Strophalosia inexpectans* Cooper and Grant (1975) from the Guadalupian of Texas may be an *Echinalosis*; however, the generic



diagnosis may have to be modified to incorporate a form with such fine spines. *Echinalosia* also appears to be present in Kungurian faunas of the Ussuriland (in the form of *Strophalosia? paradoxa* Fredericks 1925).

Two subgenera are recognised within the genus, as discussed below. *Echinalosia prideri* (Coleman) is retained within the nominal subgenus.

***Echinalosia* (*Echinalosia*) *prideri* (Coleman, 1957)**

Fig. 5A-Z

1943 *Strophalosia jukesi* Prendergast, p. 47, pl. 5, figs 18-20

1957 *Strophalosia prideri* Coleman, p. 116, pl. 18, figs 15, 16; pl. 19, figs 1-19

1967 *Strophalosia prideri* Coleman, Condon, p. 149

1976 *Strophalosia prideri* Coleman, Waterhouse, p. 99

HOLOTYPE: CPC 1018, complete shell, from right bank of Lyndon River, 14.4 km east of Mia Mia Homestead, Carnarvon Basin. Originally mapped as Bulgadoo Shale; subsequently mapped as Madeline Formation.

MATERIAL, LOCALITIES AND AGE: CPC 24497a-24497c, three shells and two isolated dorsal valves from BMR locality ML87, 13.6 km on a bearing of 82° from Mia Mia Homestead, north bank of Lyndon River, Madeline Formation. CPC 24498a-24498c, two shells and one isolated dorsal valve from BMR locality ML88, as for ML87, middle fossiliferous horizon, Madeline Formation. CPC 24415, 24416, 24499a-24499b, four shells from BMR locality F17721, 14.4 km east of Mia Mia Homestead, right bank of Lyndon River, type locality of species, Madeline Formation. CPC 24417, 24500a-24500b, two internal moulds of complete shells and one ventral valve internal mould from BMR locality WB51, 3.6 km on a bearing of 225° from Keogh Hill, lower part of Madeline Formation. All Carnarvon Basin. All Early Baigendzhinian (Late Artinskian).

SIZE RANGES: Ranges are based on 38 measured specimens (including the 15 figured specimens). Hinge width, 11.1-26.8 mm; maximum width 16.4-51.0 mm; ventral valve height, 13.8-42.9 mm; dorsal valve height 11.4-36.8 mm; thickness, 11.6-19.5 mm (based on 6 specimens—most are crushed); ventral interarea height, 1.8-4.8 mm; dorsal interarea height, 1.2-2.6 mm; dorsal septum length, 9.0-15.0 mm (based on 8 specimens).

DIAGNOSIS: Large *Echinalosia*, transversely oval to subtriangular in outline. Ventral valve with convexity accentuated towards margins and with median flattening, rarely with broad shallow sulcus anteriorly in large

specimens. Ventral spines abundant, coarse and erect; dorsal spines scattered and relatively coarse. Ventral umbo prominent and pointed; hinge narrow in mature specimens.

DESCRIPTION: Shell large for genus, outline varies from transversely oval or subcircular in juvenile specimens to transversely subtriangular in mature specimens. Ventral valve strongly convex with convexity being more pronounced towards lateral margins. Ventral valve may be medianly flattened, in a few adult specimens carries broad, flattened, relatively inconspicuous sulcus anteriorly. Ventral convexity more accentuated over visceral disc, decreases anteriorly along trail. Hinge line straight, up to two-thirds maximum shell width in juvenile shells, normally less than half maximum width in adults. Maximum shell width anterior of mid-length of shell. Cardinal region of shell imparts prominent triangular appearance to shell posterior with effect increased in many specimens by posterior lateral margins of valves being straight, parallel to umbonal shoulders; resulting in a distinct subtriangular outline to many specimens. Small, pointed ears may be developed on some specimens—others lack them entirely. Ventral umbo variable in shape; normally pointed, suberect, with small cicatrix, on some specimens incurved, overhangs ventral interarea. Ventral interarea prominent, triangular; height highly variable, striated parallel to hinge and, less distinctly, parallel to shell length. Small, high, extremely narrow delthyrium bisects interarea, filled by strongly-convex pseudodeltidium.

Exterior ornamentation of ventral valve consists of spines, concentric growth lamellae; lamellae consist of well-spaced major lamellae and closely-set (often worn, removed) fine growth lines. Spines developed as row along hinge, subconcentric rows across venter of shell. Spacing of spines a little closer over lateral margins of valve than across valve centre. Lateral spines tend to be suberect, point laterally and posteriorly. Remainder of ventral spines erect, point anteriorly. Lateral spines grade into venter spines, no discrete demarcation occurs between them. Spines vary in coarseness over valve but may be up to 1 mm thick with spine bases up to 1.5 mm thick. Some spines on anterior of largest shells may be fine (0.6 mm wide), adjacent to coarser spine. Normally about 14 spines per cm² at 2-3 cm from umbo, spaced every 4 to 7 mm along concentric row. Body spines apparently quite long, longest measured being 5 mm.

Exterior ornament of dorsal valve consists of distinct, relatively widely spaced, concentric growth lamellae, numerous spines (finer than those of ventral valve) and

Fig. 5—A-Z, *Echinalosia* (*Echinalosia*) *prideri* (Coleman). All from Madeline Formation, Carnarvon Basin. A-B, CPC 24497a, shell in dorsal and ventral views, $\times 1.2$ and $\times 1.3$ respectively. C-D, CPC 24498a, shell in dorsal and ventral views, $\times 1.3$ and $\times 1.2$ respectively. E-F, CPC 24498b, shell in dorsal and ventral views, $\times 1.2$. G-H, CPC 24499a, shell in ventral and dorsal views, $\times 1.2$. I-J, CPC 24499b, shell in ventral and dorsal views, $\times 1$. K-L, CPC 24416, shell in dorsal and ventral views, $\times 1$. M-O, CPC 24497b, shell in ventral, dorsal and lateral views, $\times 1.2$. P-Q, CPC 24500a, internal mould of shell in ventral and dorsal views, $\times 1.2$. R, CPC 24500b, internal mould of ventral valve, $\times 1.2$. S, CPC 24498c, dorsal valve interior view, $\times 1.1$. T, CPC 24497c, dorsal valve interior view, $\times 1.1$. U-V, CPC 24415, shell in ventral and dorsal views, $\times 1$ and $\times 1.2$ respectively. W, CPC 24497d, dorsal valve interior view, $\times 1.1$. X, CPC 24497e, decorticated shell in dorsal view, $\times 1.2$. Y-Z, CPC 24417, internal mould of shell in ventral and dorsal views, $\times 1.1$.

scattered subcircular dimples. Spines arranged in concentric rows, may be up to 0.7 mm thick at their base, erect, up to 5 mm long. Deoortication of valve removes most spines, leaves coarser concentric lamellae and widely scattered dimples. Dimples tend to be circular to subcircular (slightly longer than wide), normally scattered along concentric rows. Capillae have not been observed on best preserved specimens.

Ventral teeth strong, robust, divergent but set relatively close together because of narrow delthyrium. Low marginal ridge developed either side of teeth, persists anteriorly in only mature specimens as low, broad ridge around anterior perimeter of valve. Adductor muscle scars elongate, on a raised platform; normally bisected by median groove, although one specimen shows median ridge, smooth or feebly striate longitudinally. Diductor scars large, flabellate, weakly impressed anteriorly, posteriorly smooth, anteriorly striate, extend further anteriorly than adductor scars. Remainder of valve interior smooth or finely pitted.

Dorsal valve smoothly geniculate with geniculated angle being curved up to about 40° from anterior of gently internally-convex visceral disc. Dorsal interarea distinct, high, striated parallel to hinge line; bisected by sharply concave chilidium, wider than corresponding pseudodeltidium. Dorsal adductor scars smooth, bisected by median septum so that each half triangular shaped. Anterior components of adductor scars raised above level of visceral disc, posterior components depressed, lower than level of visceral disc. Brachial ridges distinct in mature specimens, arise close to anterior of posterior components of adductor scars; broadly semi-circular, hook back sharply at their anterior extremities. Region of brachial ridges smooth. Cardinal process strong, erect, extends behind hinge line, coplanar with dorsal interarea or diverges posteriorly by some 10-15°. Process quadrilobed anteriorly, prominent median lobe divided by deep groove; lateral lobes of process distinct, project widely from bisected median lobe. Cardinal process arises from strongly-developed median septum and a pair of low marginal ridges that run around deep sockets and die out on lateral margins of valve. Median septum strong, sharp, high (usually lower between adductor scars), extends for about half valve length. Anterior of valve interior distinctly pustulose.

DISCUSSION: *Echinalosia prideri* was well described by Coleman (1957) who also discussed such features as the variable nature of the ventral umbo and the height of the ventral interarea. The new material to hand indicates few changes to Coleman's description of the species. The

ventral umbo can rarely be overturned over the interarea and one juvenile specimen indicates that the cicatrix can rarely attain a large size (just over 0.5 cm at the largest diameter).

Echinalosia sp. (Waterhouse 1969) from Arctic Canada is a large form differing from *Echinalosia prideri* in possessing a distinct sulcus, more densely-spinose ventral valve and a wider hinge line.

Eastern Australian species of *Echinalosia* such as *E. preoalis* (Maxwell 1954, pl. 54, figs 1-19) and *E. ovalis* (Maxwell 1954, pl. 57, figs 4-14) are more circular species than *E. prideri* and possess relatively wide hinges (see also Dear 1971, pl. 3, figs 11-16, *Echinalosia minima* Dear 1971).

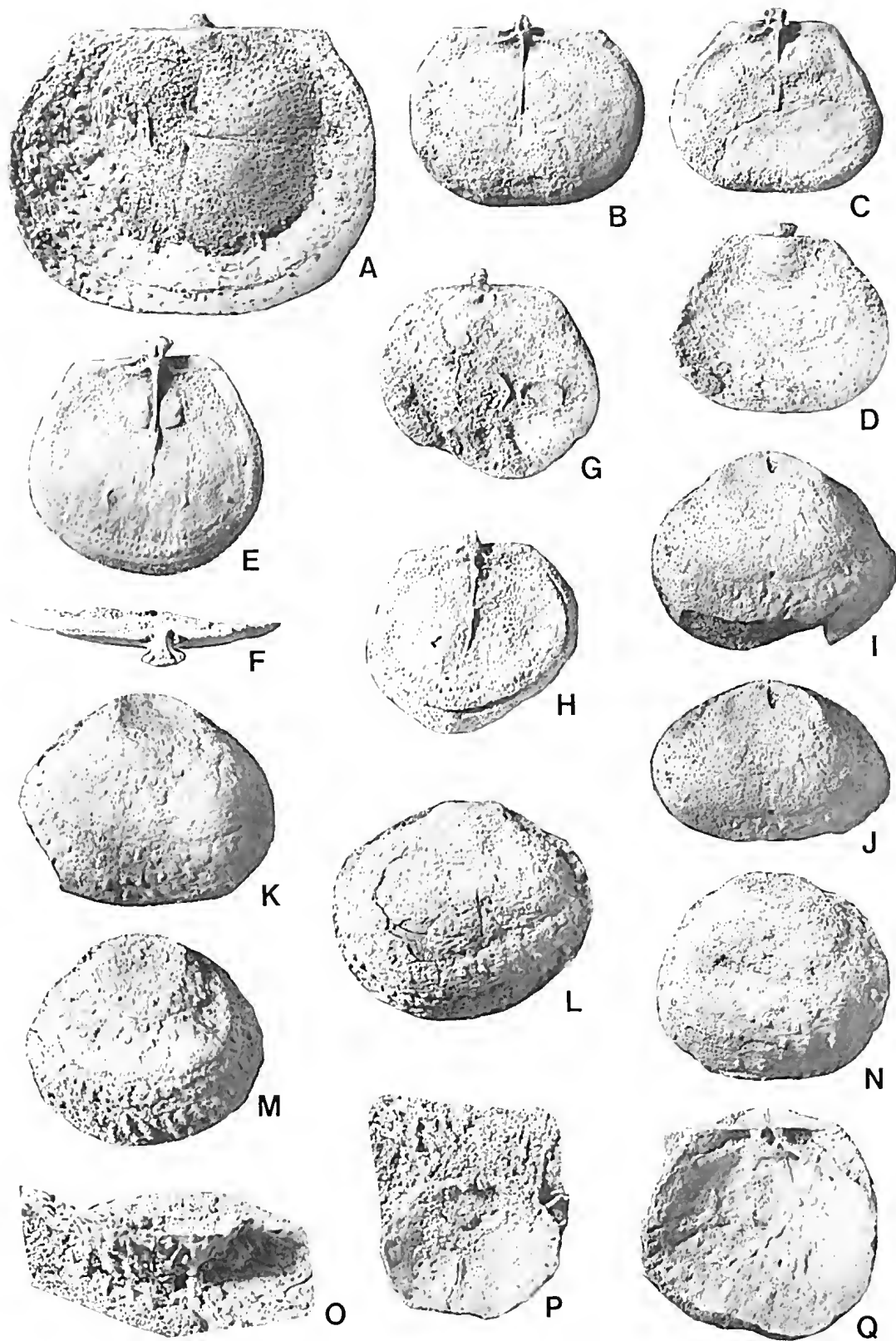
The same is also true of *Echinalosia* from New Zealand as described and figured by Waterhouse (1964). Waterhouse (1982a, sec p. 31 for synonymy) has reported in many papers that *E. prideri* is a characteristic zone fossil of Mangapirian (Late Artinskian) faunas of New Zealand. However, specimens of the New Zealand form are limited in number and preservation and only one specimen has been figured (Waterhouse 1982, pl. 23, fig. i). The figured specimen is an internal mould of a ventral valve which may indicate a species related to *E. prideri* but until the dorsal valve of the New Zealand species is known and larger collections are available, the identity of the species is in considerable doubt.

Subgenus *Echinalosia* (*Notolosia*) subgen. nov.

TYPE SPECIES: *Echinalosia* (*Notolosia*) *dickinsi* sp. nov.
DIAGNOSIS: Concavo-convex strophalosiids with circular to subcircular outline. Shell not thickened. Cicatrix large. Ventral spines adherent, semi-recumbent and erect. Dorsal spines erect, minute and abundant. Ventral interarea relatively high with high but narrow pseudodeltidium. Teeth small. Cardinal process high, erect, with prominent bisecting groove and pit on interior face; quadrilobed at maturity.

DISCUSSION: Specimens of the type species have previously been referred to *Heteralosia* (Coleman 1957) but larger collections show that the species possesses numerous minute, scattered, dorsal spines unlike that genus. Slight erosion of the dorsal valve removes all trace of the spines but leaves the lamellose growth lines. The species shares many features with *Echinalosia* Waterhouse and hence is placed in that genus but characters such as the large cicatrix and long, adherent spines indicate considerable differences from *E. maxwelli* (Waterhouse 1964) the type species of *Echinalosia*, hence the new subgenus is proposed.

Fig. 6—A-Q, *Echinalosia* (*Notolosia*) *dickinsi* sp. nov. All from Hardman Formation, Canning Basin. A-B, CPC 24451, holotype, dorsal valve in dorsal and ventral views, $\times 3$ and $\times 2$ respectively, with attached internal mould of *Neochonetes* (*Sommeriella*) sp. nov. C-D, CPC 24452, dorsal valve in ventral and dorsal views, $\times 2.2$ E-F, CPC 24453, dorsal valve in ventral and posterior views, $\times 2$ and $\times 3$ respectively. G-H, CPC 24454, dorsal valve in dorsal and ventral views, $\times 2.2$. I-J, CPC 24468, natural cast of ventral valve in ventral and posterior views, $\times 1.5$. K, CPC 24469, natural cast of ventral valve in ventral view, $\times 1.6$. L, CPC 24470, natural cast of ventral valve in ventral view, $\times 1.8$. M, CPC 24471, natural cast of ventral valve in ventral view, $\times 1.8$. N, CPC 24472, natural cast of ventral valve in ventral view, $\times 1.6$. O-P, CPC 24460, ventral valve in anterior and dorsal views, $\times 2.8$ and $\times 2.6$ respectively. Q, CPC 24462, ventral valve adherent within ventral valve, $\times 3$.



Echinalosia (*Echinalosia*) Waterhouse (1967) is a larger subgenus of subtrigonal or subcircular outline and with scattered dorsal spines. Internal features such as muscle scars and brachial ridges are more strongly developed in *Echinalosia* (*Echinalosia*), which also has a consistently, considerably smaller cicatrix of attachment than *Echinalosia* (*Notolosia*) subgen. nov. No other species is at present referable to *Echinalosia* (*Notolosia*).

Orthothrix Geinitz (1847a, 1847b) is a smaller genus with numerous, minute dorsal spines but is characterised by a trigonal outline, fine recumbent ventral spines, a short dorsal median septum and a less convex ventral valve.

Wyndhamia Booker (1929) possesses fine dorsal spines but at maturity, shells are large and subquadrate in outline. There is no evidence at present to suggest that *Echinalosia* (*Notolosia*) *dickinsi* sp. nov. is only known from juvenile material. Large strophalosiids occur with representatives of the species but they are representatives of a large new genus that lacks dorsal spines and that will be described in a subsequent study.

***Echinalosia* (*Notolosia*) *dickinsi* sp. nov.**

Figs 6A-Q, 7A-S

1957 *Strophalosia* (*Heteralosia*) *prendergastae* Coleman, (partim.), p. 127, pl. 20, figs 29-35, (non cet.)

1958 *Strophalosia* (*Heteralosia*) *prendergastae* Coleman, Guppy *et al.*, p. 54

1961 *Strophalosia* sp. Dickins, pp. 284, 287

ETYMOLOGY: For Dr J. M. Dickins of the Bureau of Mineral Resources, Geology and Geophysics, for his extensive contributions to the knowledge of the Western Australian Permian record.

HOLOTYPE: CPC 24451, an isolated dorsal valve from BMR locality KLB 11, Hardman Formation, Canning Basin.

MATERIAL, LOCALITIES AND AGE: CPC 24451-24467, nine isolated dorsal valves and eight isolated ventral valves from BMR locality KLB 11, Mount Hardman, from beds about 1.2 m thick at about 40 m below the top of the hill, Hardman Formation. CPC 24468-24472, five natural casts of ventral valves from BMR locality N1241, Lat. 19°06'39"S, Long. 125°11'27"E, Hardman Formation, Canning Basin. Chhidruan (Early Tatarian).

SIZE RANGES: e=estimate. Ranges are based on 34 measured specimens (including the 22 figured specimens). Hinge width, 5.8-15.5e mm; maximum width, 10.1-26.5 mm; ventral valve height, 8.8-22.5 mm;

dorsal valve height, 9.8-20.0 mm; thickness, 3.5-12.1 mm; ventral interarea height, 1.1-2.8 mm; dorsal interarea height, 0.6-1.5 mm; dorsal septum length, 5.5-11.6 mm.

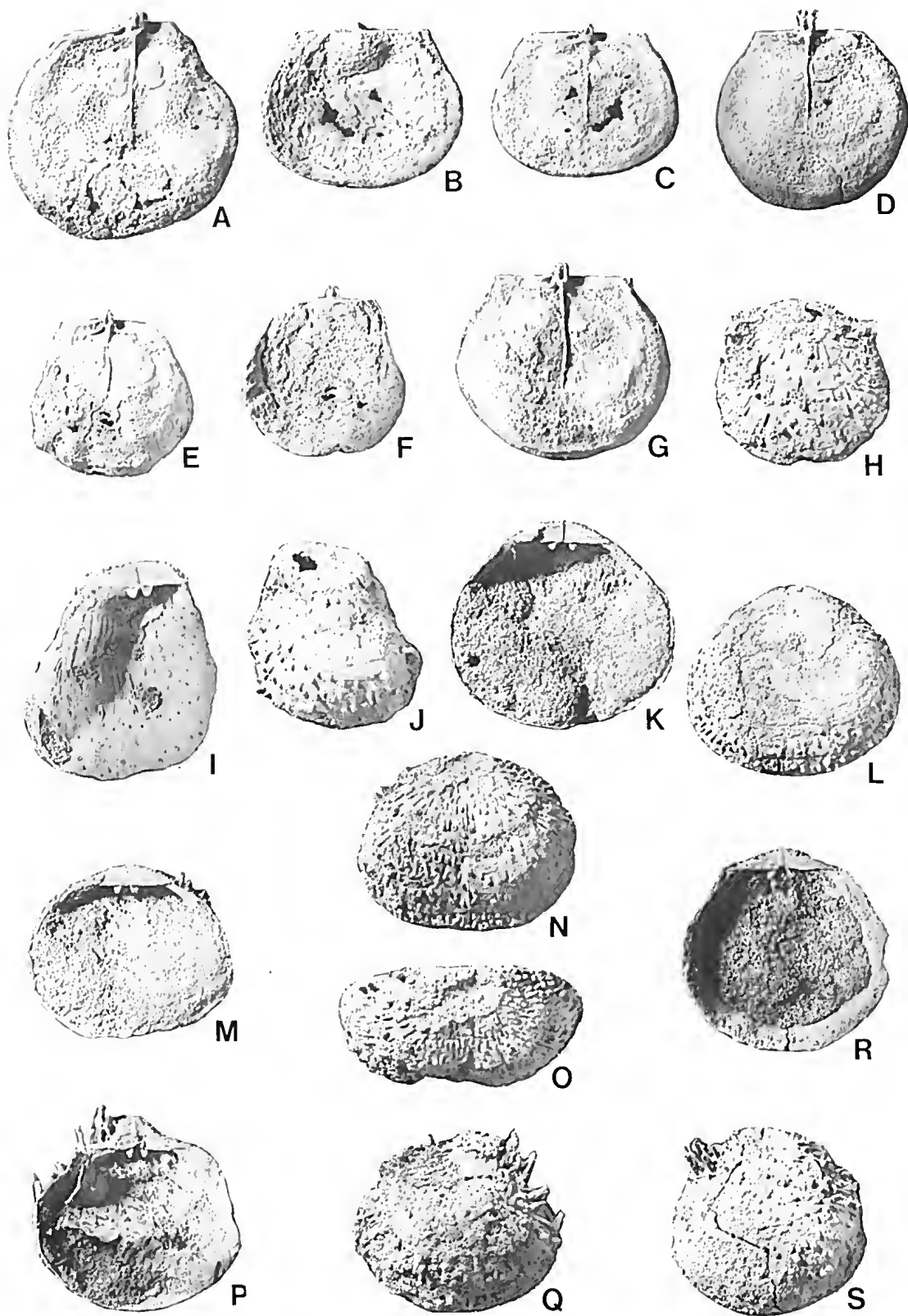
DIAGNOSIS: Small to medium sized shells with narrow hinge line and transversely oval outline in maturity. Cicatrix large. Ventral exterior ornament of concentric lamellae and fine, abundant, scattered to subconcentrically arranged spines. Dorsal exterior with minute scattered spines, scattered dimples, and concentric growth lamellae.

DESCRIPTION: Shell of moderate size with transversely oval outline at maturity. Hinge width varies from two-thirds of maximum width in juvenile stages of ontogeny to one half maximum width at maturity. Hinge extremities rounded at maturity, finely pointed in juvenile specimens. No ears developed. Ventral valve strongly convex with convexity being even. Maximum width at about two-thirds of length of shell, from umbo, at maturity. Umbo flattened by cicatrix of attachment which is large in size (largest being on specimen CPC 24468, 8.7 mm wide 7.3 mm long). Ornamentation of ventral valve consists of spines and concentric lamellae with the latter widely spaced and best seen on anterior of valve. Spines closely spaced, numerous, those over posterior lateral flanks more closely spaced than those over venter. No distinct row developed along hinge, although spines extend up to hinge. Cicatrix occupies large portion of umbonal and posterior hinge region. Spines spaced at 1 to 2 mm intervals over venter in subconcentric bands and arc from 0.2 to 0.4 mm thick. Larger specimens appear to have coarser spines anteriorly but this may in part be because of nature of preservation (as natural ferruginous casts). Posterior spines adherent to substrate, although they are long and lift juvenile shell from substrate (specimen CPC 24460).

Interareas distinct, flat, extend full width of hinge, relatively high. Ventral interarea striated parallel to hinge, bisected by narrow, triangular delthyrium filled by flat pseudodeltidium. Pseudodeltidium inconspicuous when entire. Dorsal interarea about half height of ventral interarea, weakly striate parallel to hinge line, bisected by narrow, flat chilidium.

Dorsal valve flat or gently convex during earliest stages of ontogeny, becomes gently concave subsequently. Anterior of dorsal valve distinctly, but not sharply, geniculated. Concentric lamellae distinct. Dimples scattered over valve surface. Concentric lamellae and growth lines carry rows of minute spines (up to 0.6 mm apart and 0.2 mm thick). Spines may be totally removed from valve without loss of lamellae.

Fig. 7—A-S, *Echinalosia* (*Notolosia*) *dickinsi* sp. nov. All from Hardman Formation, Canning Basin. A, CPC 24455, dorsal valve in ventral view, $\times 2$. B-C, CPC 24456, dorsal valve in dorsal and ventral views, $\times 2.8$ and $\times 2.5$ respectively. D, CPC 24457, dorsal valve in ventral view, $\times 2$. E-F, CPC 24458, dorsal valve in ventral and dorsal views, $\times 2.6$. G, CPC 24459, dorsal valve in ventral view, $\times 2.2$. H, CPC 24462, ventral valve in ventral view, $\times 2.2$. I-J, CPC 24463, ventral valve in dorsal and ventral views, $\times 3$ and $\times 2.5$ respectively. K-L, CPC 24464, ventral valve in dorsal and ventral views, $\times 1.5$. M-O, CPC 24465, ventral valve in dorsal, ventral and posterior views, $\times 1.6$, $\times 1.8$, and $\times 2$ respectively. P-Q, CPC 24466, ventral valve in dorsal and ventral views, $\times 2$. R-S, CPC 24467, ventral valve in dorsal and ventral views, $\times 1.8$.



Ventral teeth small, weakly divergent, protrude from under ventral interarea. No marginal ridge developed. Adductor scars situated high under umbo, smooth and lobate. Diductor scars poorly known but appear weakly striate.

Cardinal process arises from strong median septum and two minute lateral ridges which surround small but narrow and deep sockets. Process a small, bilobed spike in juvenile specimens and a pronounced quadrilobed, erect eminence in mature valves. It extends posteriorly at small angle to plane of dorsal interarea.

Smooth dorsal adductor scars distinct, particularly in mature specimens, and raised above level of visceral disc; bisected by median septum, not differentiated into anterior and posterior components even in largest specimen. Median septum usually from 0.5 to 0.6 length of dorsal valve, thin and sharp. Abundant papillae occur around anterior of valve. Brachial ridges only weakly developed in largest dorsal valve.

Discussion: Several small specimens of this species, figured by Coleman (1957, pl. 20, figs 29-35) as *Heteralosia prendergastae* are referred to *E. (N.) dickinsi* sp. nov. on the basis of ventral spinosity, cicatrix type and dorsal interior. Dickins (1961) recorded *Strophalosia* sp. from the Hardman Formation which appears to refer to the present species. *Echinalosia (Notolosia) dickinsi* sp. nov. is a distinctive species because of its large cicatrix, ventral spine arrangement and minute dorsal spines. Comparison may be suggested with representatives of *Echinalosia (Echinalosia)*, but in addition to comments noted above, that subgenus possesses dorsal adductor scars that are differentiated into anterior and posterior components, unlike the present species.

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Dr G. A. Thomas read an earlier version of the manuscript; Mrs I. Munro typed the manuscript and Mrs L. Archbold assisted with photography.

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THE IMPACT OF SEVERE FROST ON MALLEE EUCALYPTS, *BANKSIA ORNATA* AND *LEPTOSPERMUM CORIACEUM* AT WYPERFELD NATIONAL PARK

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ABSTRACT: The severe frosts of 1982, perhaps interacting with the ensuing drought, had dramatic immediate effects on *B. ornata*, *L. coriaceum* and the mallee eucalypts. Except for sporadic survivors, all adult *B. ornata* in frost-affected swales were eliminated. Seed from frost-affected cones shows poor germination, even after subsequent fire. *L. coriaceum* showed high and variable kills of standing foliage, but the population is recovering from coppice and suckers, even in the worst-affected areas. Mallee eucalypts responded to frost damage by coppicing in a pattern related to the severity of the damage. Very few seedlings established in the frost-killed areas, the majority of which lie in bare ground outside the litter layer.

In June and July of 1982, very severe frosts were experienced in parts of Wyperfeld National Park (Table 1). Although periods of winter frost are common in this region, nothing of this severity has been recorded since detailed climatic records were initiated in 1959 at the Ranger's residence. Data for Ouyen, which date back to the early 1900s, suggest that frosts of this severity may be very rare occurrences. The 1982 frost was accompanied by a severe drought, the worst since 1959. The annual rainfall (108 mm) was only 30% of the annual average (351 mm) and the rainfall data collected at the Ranger's residence show that from July 1982 to February 1983, no month had more than 10 mm and the total precipitation was only 30.5 mm (Table 2). Data for Rainbow show 1982 as the lowest rainfall since records began in 1901, again with only 29 mm in the same period.

The impact on the vegetation was dramatic. Thousands of hectares of mallee scrub and heathland were devastated, especially in the interdune swales. Adult *Banksia ornata* and *Leptospermum coriaceum* were severely affected in the heathlands, while *Eucalyptus in- crassata*, *E. dumosa* and *E. foecunda* showed distinctive

effects in the scrublands. Areas rich in these species were selected for detailed study in 1985.

Preliminary investigations showed that frost-killed banksias failed to regenerate by coppicing. Very few seedlings were encountered in these areas and the majority of follicles on the cones of frost-killed bushes remained closed. Healthy flowering banksias were found on dune crests and occasionally as survivors in swales. Since the majority of frost-affected banksias were dead it was decided to evaluate the status of the seed reserves held in the frost affected cones and to study the response of leaves of *Banksia* to an experimental freezing treatment.

Stands of frost-affected *L. coriaceum* showed many adults had been killed. Many plants were coppicing from the base of dead stems, or producing suckers from lateral roots. In many cases, this coppice regrowth was itself dead or dying. Seedlings were infrequent. It was decided to assess the impact of freezing on seeds in capsules of *L. coriaceum*, the impact of experimental freezing on adult and seedling foliage, and the severity of frost-induced injury at field sites.

Frost-affected mallee eucalypts showed typical coppice regrowth: death of adults was rare. Severely-

TABLE 1
MINIMUM TEMPERATURES (°C: SCREEN DATA) WYPERFELD RANGER'S RESIDENCE

JUNE 1982														JULY 1982													
Date	4	5	6	7	8	9	15	16	17	18	19	20	21	22													
Temperature	-5.0	-8.0	-8.0	-7.0	-6.0	-5.0	-1.0	-5.0	-7.0	-1.0	+3.0	-6.0	-8.0	-6.0													

TABLE 2
MONTHLY RAINFALL RECORDS (mm) WYPERFELD RANGER'S RESIDENCE

	J	F	M	A	M	J	J	A	S	O	N	D	TOTAL
1982	14.6	13.5	12.0	12.0	14.4	17.3	4.3	9.9	5.2	2.1	1.2	2.0	108.5
1983	5.8	0	99.5	21.7	35.0	21.2	35.4	59.8	53.6	57.4	21.1	55.0	465.5

affected trees, in which the whole of the canopy had been destroyed, coppiced mainly from the lignotuber; less severely-affected trees coppiced along the length of the stems. Seedlings were rare. It was decided to evaluate the impact of experimental freezing treatments on seed viability in the capsule and when shed, and the distribution and number of seedlings beneath frosted eucalypts.

METHODS

SEED COLLECTION

Capsules of *Leptospermum* were collected from healthy, apparently unfrosted plants on the upper slopes of Eastern Lookout and Flagstaff Hill (Fig. 1). Green and brown capsules occurred on those bushes, green capsules being the products of the last flowering period, brown capsules being from earlier flowering periods. Seed was extracted by allowing capsules to open at room temperature in paper bags and then rubbing opened capsules firmly between the palms of the hand. Seeds were separated from chaff.

Cones of *Banksia* were collected along Nine Mile Square Track, either from adults killed by frost or from undamaged bushes flowering at the time. Seed was released by heating cones in an oven at 200°C for 1 hour or by setting fire to cones on a BBQ grill and removing them as follicles opened and before the seeds were lost.

Capsules of *E. incrassata* were collected from Eastern Lookout, *E. dumosa* from the Lowan Track and *E. foecunda* from the Dattuek Track (Fig. 1), in all cases from long unburnt and unfrosted stands. Seed was extracted by placing capsules in an oven at 30°C for 2-3 days; chaff was separated from seed.

SEED GERMINATION AND SEED VIABILITY

All attempts to germinate seeds of *B. ornata* and *L. coriaceum* on filter paper, with or without surface sterilization, were unsuccessful. Two artificial, sterilized soil mixes gave highly variable results. Accordingly, viability was estimated by placing seeds sliced through the embryo in 0.1% tetrazolium violet in phosphate buffer at pH 6.8 in the dark for 45 minutes. Viable embryos turn red (Moore 1973).

The seeds of all three eucalypt species were germinable on filter paper. Seeds were germinated in sets of 100 (5 × 20 per dish) held at 25°C in a 12 hour light/dark cycle, for 40 days at 60 μE m⁻² sec⁻¹ (Grolux fluorescents). Germinated seeds were removed every 2-3 days. This method yielded high results for *E. incrassata* (93% germination) and *E. dumosa* (99%) but gave variable results (58%, 33%, 77%) with *E. foecunda*. *E. foecunda* gave high results (94%) when germinated in the same manner but at uncontrolled room temperatures in fluctuating light conditions. Preliminary trials with *E. incrassata* showed no differences between seeds from younger and older capsules. Tests on *E. incrassata* and *E. dumosa* showed no significant differences between seed lots from different trees (*E. incrassata*, 7 trees; *E. dumosa*, 3 trees), so pooled seed samples were used throughout.

SIMULATED FROST TREATMENTS

Seed and Capsules

Capsules of *L. coriaceum* were divided into three groups: one was used as a control, one group was frozen once and the third group twice over two days at -20°C for 8 hours. This experiment was repeated six times. 50 seeds per treatment were assessed for viability.

Unopened eucalypt capsules or seeds extracted from capsules were given one of three treatments: 1 × 4 hours, 1 × 28 hours or 7 × 4 hours, each at -20°C. Seed was extracted from frozen capsules in the normal manner. This experiment was repeated on dry and imbibed seeds (an imbibition curve for *E. incrassata* established that imbibition was complete in 30 minutes). One additional experiment was carried out on *E. incrassata* only. One hundred seeds, germinated until seed coat rupture, were exposed to 2 × 4 hours at -20°C with 20 hours between freezing treatments.

Vegetation

A portable, battery-operated fridge/freezer (ENGEL model MRFT 56.0-A4) was used to freeze either isolated shoots of *B. ornata* and *L. coriaceum* or attached branches (*L. coriaceum* only) in the period July 16-23, 1985.

Branches from each of two tagged adult *B. ornata*, one from the dune top the other a survivor in a dune swale, were collected from Nine Mile Square Track, as were seedlings that had germinated after the 1981/82 fire. Two kinds of control were used. For the adults, fresh leaves were collected daily from the tagged bushes. For the seedlings, shoots were maintained in water after the initial harvest, and fresh leaves from these shoots were measured each day. Treated plants were frozen at -20°C for 8 hours each day for 7 successive days. After removal from the freezer, the bottom 3 cm was cut from the base of each shoot under water to prevent xylem blockage. After a 2-hour thawing period, five leaves were sampled from each treatment and control. Several dozen hand sections were prepared, pooled and stained for about 2 min in 5% Evans Blue (Gaff & Okong'O-Ogola 1971). Ten sections were assessed by light microscopy for percentage cell death (dead cells stain blue, live cells remain unstained), the mean of the ten calculated and plotted as mean per cent cell death against time.

Three types of adult foliage were chosen for *L. coriaceum*: branches from a mature healthy plant (termed "stem"); healthy basal coppice regrowth (termed "basal") and healthy root-sucker coppice (termed "root-sucker"). These parts were collected separately from dune crest and dune swale. Seedling shoots were also collected from the swale as none were found on the dune crests. All these shoots were treated and maintained, controls established and percentage cell death measured as described for *B. ornata*.

A part of two mature *L. coriaceum* plants was also frozen in the field. The portable freezer was placed beside the plant, a few mature shoots were bent over into the freezer and the lid closed and fastened. The

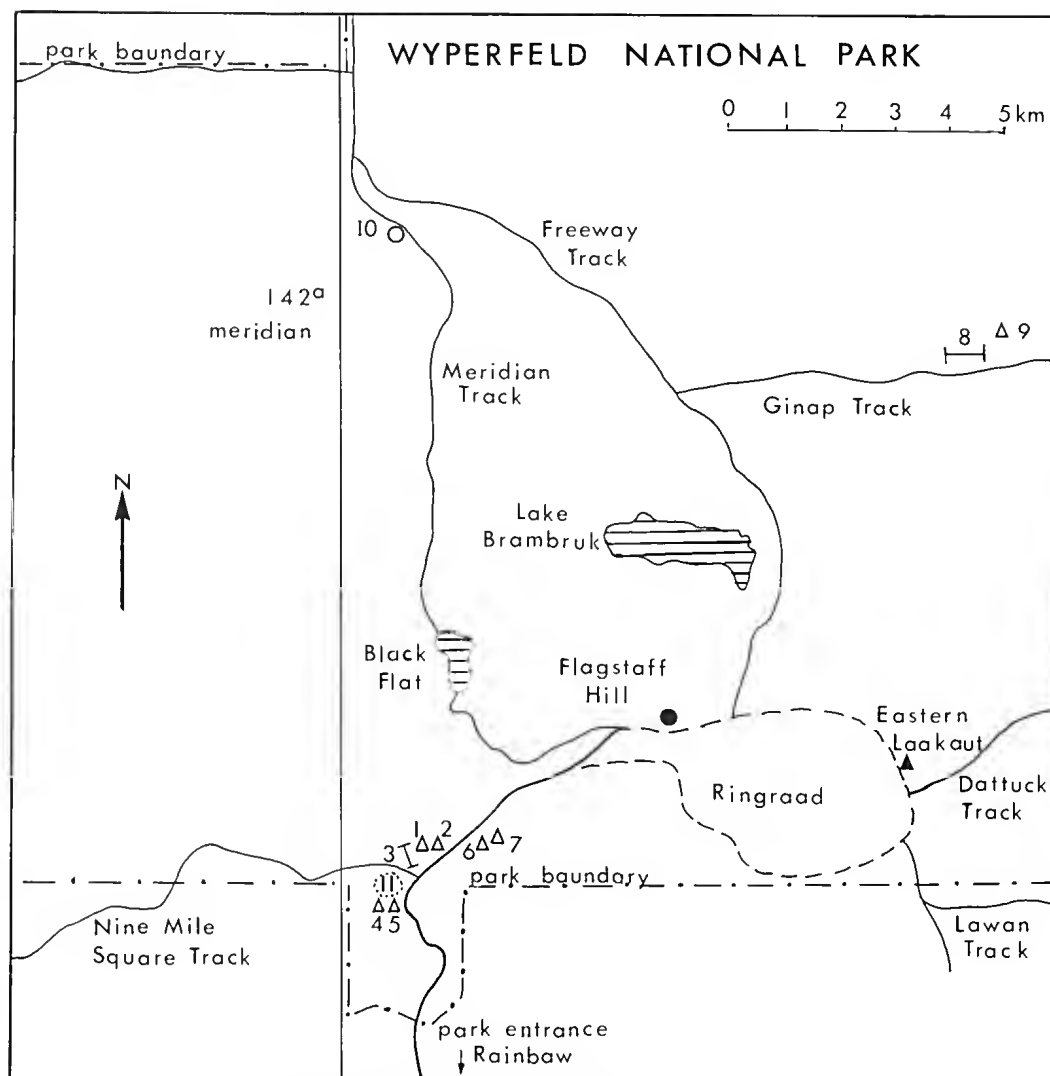


Fig. 1—Map of part of Wyperfeld National Park showing tracks and study sites. Δ *L. coriaceum* sites assessed for post-frost regrowth. \square Transects used to study seedlings induced by frost (site 3), and induced by fire in January 1981 (site 8). \circ Frost-killed *B. ornata* site, burnt by fire in January 1985. Area used to measure frequency of seedling eucalypts beneath eucalypts showing various degrees of frost damage.

shoots were given a single treatment of 8 hours at -20°C . One of the plants had green, closed capsules on its frozen branches.

FIELD MEASUREMENTS

Basal and Root Sucker Regrowth Assessments of L. coriaceum

This experiment was designed to measure the condition of the basal and root-sucker coppice regrowth of *L. coriaceum* in different areas. Basal regrowth is coppice occurring from the bottom of otherwise dead parent stems, and root sucker regrowth arises from horizontal roots.

Seven sites, all showing extensive frost damage, were chosen, four at Nine Mile Square Track (Sites 1, 2, 4, 5,

Fig. 1), one along Ginap Track (Site 9, Fig. 1) and two at a dune 4.5 km along the entrance road from the main gate (Sites 6, 7, Fig. 1). In each site, 176 plants were assessed with the percentage death of the frost-induced coppice regrowth for each plant being recorded. Some plants had no coppice regrowth on the main stems and appeared to be dead: these are recorded as "basal coppice absent". The condition of 176 root suckers was recorded in the same areas. Because open capsules were observed on frosted *Leptospermum*, seedlings were counted in a $30\text{ m} \times 30\text{ m}$ quadrat placed at random within the sites used for the coppice regrowth assessments. Though most suckers were multi-stemmed, the seedling nature of these plants was confirmed by partial excavation.

Frost-Induced Eucalypt Seedlings

A 400 m belt transect, marked every 10 m, was set out near Nine Mile Square Track (Site 3, Fig. 1). The transect began on a dune crest in an *E. incrassata* stand, and ended in an *E. foecunda* stand in a swale. Eucalypt seedlings were counted within 1 m either side of the transect line. The initial recordings were made in February 1985 and each seedling was marked by placing a coloured tag next to it. The fate of the marked seedlings was recorded finally in August 1985.

A second belt transect, 600 m long, also marked every 10 m, was set out adjacent to the Ginap Track (Site 8, Fig. 1). Part of this transect, from the 0-370 m mark, was burnt in the summer of 1981/82, before the area was exposed to the severe frosts of 1982. Again, all seedlings within 1 m of either side of the transect were recorded and marked.

In an attempt to measure the impact of frost severity on the abundance of seedlings beneath frosted trees, a frost severity scale was constructed arbitrarily as follows:

A. Severe frost: no canopy present, regrowth from lignotuber only.

B. Medium frost: no canopy, coppice regrowth from stems and lignotuber.

C. Light frost: some canopy present, stem coppice only.

D. Very light frost: nearly all canopy present, little coppice evident.

Trees with seedlings beneath them were assessed for frost severity (Site 11, Fig. 1). Next, the distribution of seedlings in relation to the tree was measured as follows. The tree was taken to be in the centre of two circles: the radius of the first gave the area covered by litter fall. The radius of the second circle minus that of the first allowed calculation of the litter-free zone beyond the litter layer in which most seedlings seemed to occur. Trees without seedlings were not measured because, in the case of the

severely-frosted categories, it was not possible to be sure that the trees had capsules on them before the frost.

RESULTS

VIABILITY OF SEEDS IN CONES OF *B. ornata*

The data are set out in Table 3.

TABLE 3
PERCENTAGE SEED VIABILITY IN 3 REPLICATE TRIALS (100 SEEDS/TRIAL): *B. ornata*.

Cone Opening Technique	Cone Type			
	Frosted	Mean	Unfrosted	Mean
Oven	74, 70, 69	71	79, 83, 85	82
Firing	85, 82, 86	84	90, 97, 86	91

A two way ANOVA was conducted using a BMDP2V program after arcsine transformation of the data. The result showed highly significant differences between the frosted and unfrosted cones ($P < 0.001$) and the technique used to open them ($P < 0.005$).

VIABILITY OF SEEDS OF *L. coriaceum*

The data are set out in Table 4.

After arcsine transformation, an ANOVA was carried out which showed highly significant effects of site and treatment ($P \leq 0.01$) and no significant effect of capsule colour. The first-order interaction of site \times capsule colour was also highly significant ($P \leq 0.01$). Since sites showed significant effects and capsule colour did not, SNK tests were done on the treatment means after pooling results across colours. Because sites were significant, the SNK test was done separately for Eastern Lookout and Flagstaff Hill. The result is shown in Table 5. Means

TABLE 4
PERCENTAGE SEED VIABILITY FOR *L. coriaceum* TREATMENTS*

Treatment	Location							
	Eastern Lookout				Flagstaff Hill			
	Replicates	Mean	\pm	sd.	Replicates	Mean	\pm	sd.
Control, Green ¹	88,73,80,84,94,68	81.2	\pm	9.6	62,53,60,56,73,57	59.2	\pm	8.1
Control, Brown ²	58,79,62,77,66,68	68.3	\pm	8.3	60,65,60,67,74,70	66.0	\pm	5.5
Frosted \times 1 ³ , Green	64,64,65,66,64,68	65.2	\pm	1.6	50,44,51,40,57,41	47.2	\pm	6.6
Frosted \times 1, Brown	56,68,55,73,58,63	62.6	\pm	7.2	48,58,46,56,49,58	52.3	\pm	5.4
Frosted \times 2 ⁴ , Green	62,60,59,58,53,53	57.5	\pm	3.7	41,46,43,40,38,37	40.8	\pm	3.3
Frosted \times 2, Brown	26,64,32,59,40,49	45	\pm	15.0	40,54,42,52,43,55	47.7	\pm	6.7

* 50 seeds measured per replicate.

1. Seed extracted from green capsules.

2. Seed extracted from brown capsules.

3. Capsules frosted for one 8-hr period at -20°C .

4. Capsules frosted twice for 8 hrs at -20°C , with 20 hrs at room temperature.

underlined are not significantly different from one another ($P > 0.05$): all other means from each site are significantly different ($P \leq 0.01$).

TABLE 5
SNK TESTS ON SEED VIABILITY OF *L. coriaceum* (DATA FROM TABLE 4)

Site	Arcsine of % Viability		
	Control	Frosted Once	Frosted Twice
Eastern Lookout	60.4	53.0	45.7
Flagstaff Hill	52.7	44.9	41.7

The SNKs show clearly that all freezing treatments reduce viability with respect to controls. However, the viability of seed frozen in capsules from Eastern Lookout is affected more by two freezing treatments than by one, but this is not true for seed from capsules from Flagstaff Hill. There, even though the mean viability is reduced by two freezing treatments, there is no significant effect of the second treatment.

FREEZING TREATMENTS ON CAPSULES OF *Eucalyptus*

The results are set out in Table 6.

TABLE 6
PERCENTAGE GERMINATION OF SEEDS* EXTRACTED FROM FROZEN CAPSULES

Species	Unfrozen Capsules	Frozen Capsules Frost Treatment		
		1 × 4 hr	1 × 28 hr	7 × 4 hr
<i>E. incrassata</i>	99	93	80	87
<i>E. dumosa</i>	99	91	71	82
<i>E. foecunda</i>	94	88	90	97

* 100 seeds measured per treatment

FREEZING TREATMENTS ON DRY AND IMBIBED SEEDS OF *Eucalyptus*

The results are set out in Table 7.

TABLE 7
PERCENTAGE GERMINATION OF SEEDS* FROZEN EITHER DRY OR IMBIBED †

Species	Unfrozen Seed	Frozen Seed					
		1 × 4 hr		1 × 28 hr		7 × 4 hr	
		DryImbibed	DryImbibed	DryImbibed	DryImbibed	DryImbibed	DryImbibed
<i>E. incrassata</i>	99	98	97	98	97	95	37
<i>E. dumosa</i>	99	91	92	85	98	94	30
<i>E. foecunda</i>	94	85	98	88	90	94	63

* 100 seeds measured per treatment.

† All seeds imbibed for 30 minutes prior to first freezing treatment.

Although the results shown in Tables 6 and 7 were not replicated, the results are very clear cut: the only treatment to reduce seed germinability is 7 × 4 hr treatments imposed on imbibed seeds (Table 7). In seeking an explanation of this phenomenon, and of the difference between *E. foecunda* and the other two species, it was noted that germination was proceeding during the 7 days over which the 7 × 4 hr treatments were administered and that *E. foecunda* was the slowest species to germinate. It seems likely that the high death rate in the 7 × 4 hr imbibed treatments was due to the onset of germination in the sample during the treatment period. To confirm that germinated seeds were frost sensitive, one hundred germinated seeds of *E. incrassata* were given 2 × 4 hr freezing treatments with a 20 hr period at room temperature between them: all seeds were killed by this treatment.

SIMULATED FROST TREATMENTS GIVEN TO VEGETATION

The results for *B. ornata* foliage are shown in Fig. 2. Adult foliage began to show rapid death after 5 repeated freezing treatments, and the source of the foliage (dune crest or swale) was without effect. Seedling foliage remained unaffected throughout the treatment period.

The results for *L. coriaceum* are set out in Figs. 3-5. The contrast with *Banksia* is quite striking. All adult tissues show significant cell death after just two freezing treatments, with tissues from swale plants being slightly more sensitive than those taken from dune crests. Interestingly, tissues from root sucker coppice take longer to die than other sources of adult foliage, independent of site. As Fig. 5 shows, seedling tissue has about the same sensitivity as adult foliage (dune crest seedlings were not available to test).

The parts of the plants frozen in the field had turned brown 4 days after exposure to the freezing treatment, producing dead branches on an otherwise healthy bush. The green capsules which were frozen on these bushes also opened after 4 days and released their seed.

RECOVERY OF FROSTED *L. coriaceum* IN THE FIELD

The data are shown in Table 8. Plants showing no regrowth are marked as "basal coppice absent".

After arcsine transformation, ANOVA's showed significant differences between sites for the death of both basal coppice regrowth and root sucker regrowth (plants without any basal regrowth were omitted from the ANOVA). Inspection of Table 8 shows clearly that most of the differences between sites are being generated by the observations at sites 5 and 6, which are markedly different from the other five sites. The percentage of plants showing no basal regrowth also shows marked site to site variation, and again it is sites 5 and 6 which lie at extremes of the range.

FROST INDUCED EUCALYPT SEEDLINGS

Results from the Belt Transects

Only 6 seedlings (3 of *E. foecunda* and 3 of *E. incrassata*) were encountered in the 400 m of belt transect through the frosted area at Nine Mile Square Track, and

TABLE 8
PROPORTIONS OF COPPICE PLANTS OF *L. coriaceum* SHOWING VARYING DEGREES OF SUBSEQUENT DEATH AT EACH OF SEVEN SITES⁴.

% of Regrowth Shoots Dead	% of Plants at Each Site (n = 176)							Mean
	1	2	3	4	5	6	7	
1. Basal Coppice ¹ 0	49.4	46.0	38.6	53.4	18.2	7.4	42.6	36.5
1-25	16.5	30.1	8.5	5.1	79.5	2.3	31.3	24.8
26-50	6.3	5.7	5.1	3.4	1.1	1.7	0	3.3
51-75	0	0	0.6	0.6	0	0	0	0.2
76-100	4.5	4.5	8	1.1	0.6	6.3	0.6	3.7
Basal Coppice Absent ²	23.3	13.6	39.2	36.4	0.6	82.4	25.6	31.6
2. Root Sucker Coppice ³ 0	65.3	70.5	71.6	80.1	48.3	55.7	83.0	67.8
1-25	28.4	25.0	19.3	16.5	50.0	36.4	16.5	27.4
26-50	3.4	2.8	2.8	2.3	0	5.7	0.6	2.5
51-75	0	1.1	0	0	0	0	0	0.2
76-100	2.8	0.6	6.3	1.1	1.7	2.3	0	2.1

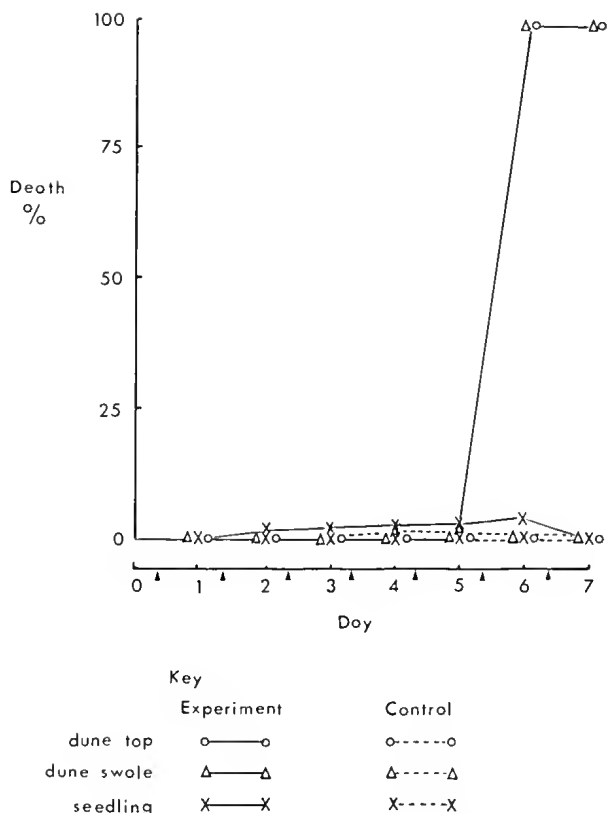
1. Regrowth from base of main stem.

2. No regrowth off main stems, which appear to be completely dead.

3. Regrowth from horizontal roots.

4. All sites are in areas of severe frost kill where the only surviving foliage⁵ is from coppice shoots (see Fig. 1).

5. Seedling counts in the same sites (30 m × 30 m quadrat) were 0, 0, 1, 44, 5, 0, 16.



only 4 of these survived till August of 1985 (all still alive 18/2/86).

At Ginap Track, 200 m of the belt transect passed through a patch of vegetation burnt in the summer of 1981/82. This region had 169 seedlings (all *E. foecunda*) that are all the result of the fire (no plant tops survived the fire to act as a seed source during the frost periods). Unfortunately, it is not known precisely when those seedlings germinated. They may be the survivors of germinants induced by the regular low monthly rainfalls from January 1982-June 1982 (average of 14 mm/month: see Table 2). Alternatively, they may not have germinated till the autumn of 1983, following the drought-breaking rains (99.5 mm) of March 1983. Of the 169 seedlings present on 21/2/1985, 158 were still alive at 4/8/1985 (122 at 18/2/1986). The significance of these points is brought out in the discussion.

Distribution of Seedlings Beneath Frost Affected Trees

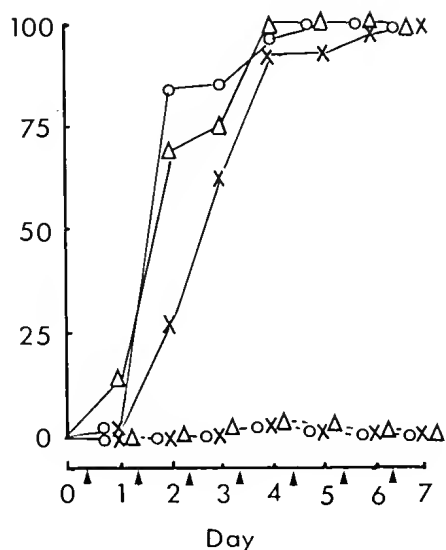
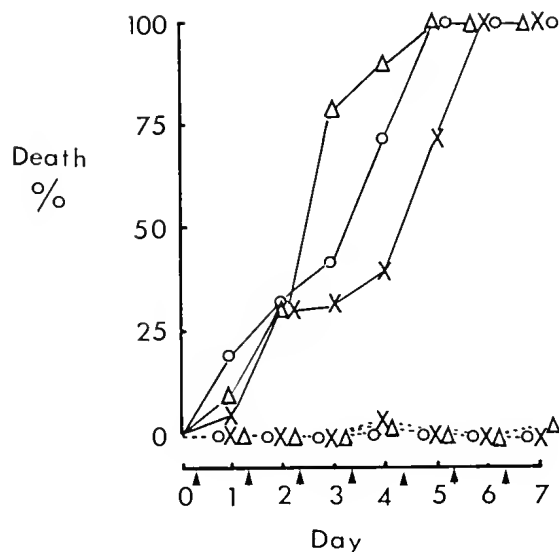
The results are set out in Table 9. All observations were made in an area near to the location of the belt transect at Nine Mile Square Track (Site 11, Fig. 1).

Clearly, all of the seedlings were found in the unlit areas outside of the litter layer. The number of seedlings per square metre does not vary in any regular manner with the degree of frost damage experienced by the putative parental tree.

DISCUSSION

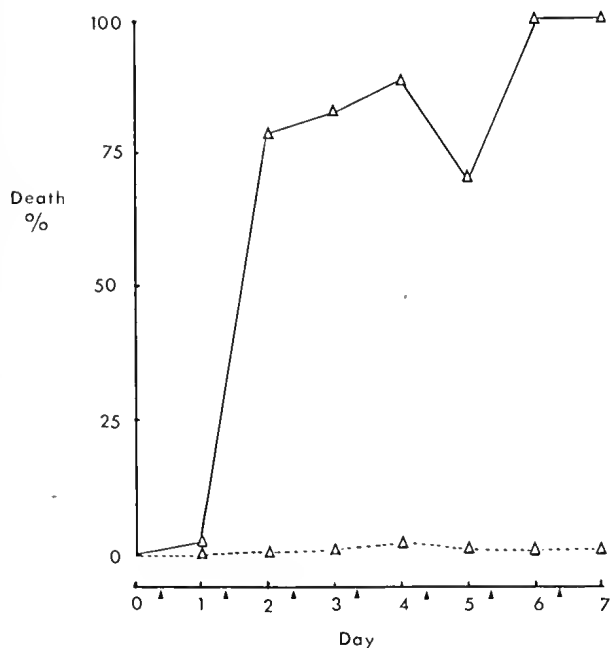
1982 saw two unusual climatic events impact upon Wyperfeld National Park. Two extended periods of severe frost with screen temperatures dropping to -8°C

Fig. 2—Percentage of dead cells in leaf tissues of adult and seedling *B. ornata*, following successive freezing treatments at -20°C . The freezing treatments were given at the arrows.



Key

Experimental	Control
stem ○—○	○-----○
root sucker x—x	x-----x
basal △—△	△-----△



Key

Experimental	Control
△—△	△-----△

Figs 3-5—Percentage cell death induced by successive freezing treatments at -20°C on leaf tissues of *L. coriaceum*. Three types of adult foliage were used: leaves from an undamaged mature plant ("stem"); leaves from healthy basal coppice regrowth ("basal"); leaves from healthy root-sucker coppice ("root-sucker"). Figs. 3 and 4 show the effects on leaves taken from dune top (Fig. 3) and dune swale (Fig. 4). Fig. 5 shows the results from seedlings from the swale (none were available to test from dune tops). Freezing treatments were given at the arrows.

occurred in June and July, and were followed by the worst drought since 1959 (see Tables 1 and 2) and probably the worst since 1901 if data for Rainbow are typical of the area. Unfortunately, temperatures in the dune swales were never measured during that period and such severe conditions did not occur during the 1985 study period. The factors that generated this frost are not known, and are being examined, but it is clear from the patterns of vegetation kill and the local topography that it was not a simple matter of cold-air drainage and the local radiation effects. Anecdotal comments suggest that the temperatures in the swales may have been well below those measured in the screen at the Ranger's residence. For this reason, the temperature of -20°C was chosen to represent the worst imaginable conditions in this situation. It is also impossible to be sure how much influence the subsequent drought had on the effect of the frost. As the boundary between the killed vegetation and healthy vegetation is often very sharp, especially on dune slopes, and because there are often similar sharp

TABLE 9
DISTRIBUTION OF SEEDLINGS IN LITTER-RICH AREA AND UNLITTERED AREA BENEATH TREES SHOWING
DIFFERENT DEGREES OF FROST DAMAGE (NINE MILE SQUARE TRACK)

Frost Severity Rating	No. of Trees Sampled	Litter Area (m ²)	Seedling Number	Unlittered Area	Seedling Number	Seedlings/m ²
<i>E. incrassata</i>						
A	6	133.2	0	108.6	46	0.42
B	5	85.5	0	54.7	8	0.15
C	10	149.6	0	185.0	17	0.09
D	6	112.5	0	76.1	12	0.16
<i>E. foecunda</i>						
A	4	72.9	0	97.7	22	0.23
B	4	62.8	0	70.3	33	0.47
C	4	18.9	0	25.7	5	0.19

boundaries within the canopy of a single tree, we incline to the view that most of the damage was done by the frost. The impact on *B. ornata*, *L. coriaceum* and the mallee eucalypts is discussed separately.

B. ornata

In many parts of the Park, the only surviving adult specimens are now located on dune crests and upper dune slopes above the level affected by the frosts. Large areas of seedlings established after the 1981 fires, still exist in the west of the Park along Nine Mile Square Track. Frost-killed adults failed to coppice: there are occasional adult survivors in the swales, due probably to local vagaries of frost intensity. In fact, as Fig. 2 shows, adult foliage of this species appears to be remarkably resistant to repeated freezing and thawing, even at the very low temperature of -20°C , chosen deliberately to represent the worst state that might have obtained in the swales. Five cycles of freezing and thawing were necessary before a sudden collapse of the tissue occurred. Tissues from the swale survivor did not behave differently from those of the plant from the dune crest. In agreement with field observations, seedling tissues were even more resistant (see Fig. 2), surviving 7 successive freeze/thaw cycles at -20°C . These observations help to understand how *B. ornata* survives in this frost-prone environment.

Wyperfeld normally experiences 5-15 frost days per year but in 1982, this number was 35, including the two severe periods of about a week each shown in Table 1. Presumably, the exceptional winter was more than this normally frost-hardy plant could tolerate. The basis of the resistance of this species to frost is not known. Layton and Parsons (1972) showed that consecutive 6 hr frosts to -5°C would kill 50% of 10 week old *B. ornata* seedlings that were raised in a growth cabinet. Field-grown plants seem to be much more resistant. Scanning electron microscopy confirms that a rich indumentum of coiled hairs is present on the leaves of the adult plant, and is even more strongly developed on seedlings (unpublished observation). Thomas and Barber (1974)

showed that leaves of *E. urnigera* would supercool to -10°C if their surface was kept dry, but only to -4°C if the surface was wet. Harwood (1980, 1981), working with subalpine *E. pauciflora*, supported this observation; wetted leaves showed about 16% more leaf damage than unsprayed leaves ($P < 0.01$). In those experiments, leaves began to freeze in the range -2.2°C to -6.9°C . While it is possible that the presence of hairs may modify the leaf surface microclimate and modify the effects of freezing, it is, at first sight, hard to believe that such features could allow supercooling to -20°C , the temperatures used in our experiments. However, Lindnow *et al.* (1982) have shown dramatic effects on the temperature at which leaves will freeze depending upon the presence or absence of ice-nucleating bacteria on the leaf surface. Thus, barley leaves with surfaces contaminated by *Pseudomonas syringae*, show 50% frozen cells at -3.0°C ; the same tissues taken from plants raised axenically in sterilized nutrient solutions in the absence of these bacteria required -16°C to produce the same effect. Such dramatic effects raise very interesting possibilities for desert plants and need careful evaluation with these species. Paton (1972) has shown that in *E. viminalis*, frost resistance involves more than one mechanism. In a more recent study (Paton 1981) he can find no effect of glaucousness on frost resistance in populations segregating for this character.

Cheal *et al.* (1979) list *B. ornata* as an obligate seed regenerator. Thus the fate of the *B. ornata* in the frost-killed areas clearly hinges now on its seed reserves. The state of these seed reserves is open to question. Though seed from frosted cones has a reasonably high viability in the tetrazolium test, seed from frosted cones has a significantly lower viability (84% vs 91%) than seed from unfrosted cones. More importantly, none of the seed from frosted cones would germinate. Mr A. Salkin (personal communication) says that seed germinability declines rapidly with age in this species. Certainly, thorough searches of frosted stands show very few seedlings and at site 10, where fire in 1985 burnt a large area of previously frosted *B. ornata*, seedling abundance is extremely low (4 seedlings in a 4500 m² fixed quadrat,

the survivors at April 1986 of 6 recorded in February 1986). Normally, *B. ornata* regenerates strongly after a fire (Gill 1976, 1981). It appears that the frost may induce a catastrophic reduction in the area occupied by *B. ornata* in the Park.

L. coriaceum

As Table 8 shows, of the 1232 plants counted, on average 31% were killed completely. This judgement is based on the failure of these stems to produce basal coppice in the 3 years that have elapsed since the frosts. Furthermore, about 5% of these stems were checked for signs of living bark at ground level; none was detected. An average of 60% of the plants had basal coppice showing less than 25% dieback. This species also suckers freely from its horizontal roots; stands therefore consist of groups of individuals produced initially from seedlings, each of which may have produced clones, by suckering, to an extent that has not been measured. No attempt was made to estimate the proportions of individuals attached to common root systems since preliminary excavations showed that these clones can extend over hundreds of square metres. Similarly, it is not known if suckering is affected by the degree of damage to the above-ground shoot system. Thus, we do not know if plants that failed to generate basal coppice have produced suckers which have survived, even though the "parent bush" is dead to ground level. Root suckers are abundant at all sites and their coppice is very healthy: on average, 94% of such suckers show less than 25% dieback (see Table 8). An interesting feature of these observations is the high between-site variation in the pattern of response. Sites 5 and 6 show extraordinarily low and high (respectively) proportions of dead adults: the same two sites show the lowest levels of undamaged root-sucker coppice. We have made no attempt to explore the sources of this between-site variability but will not be surprised if it is related to variations in soil moisture stresses (see Adams 1985).

The cause of the coppice dieback is likewise unexplained. Dead coppice shoots were often covered with a population of black dots which have been kindly identified by Mr I. Pascoe of the Victorian Plant Research Institute at Burnley Gardens as *Seimatosporium leptospermi*. Bagnall and Sheridan (1972) observed this fungus on *L. scoparium* in New Zealand and on *L. juniperinum* at Bayswater, Victoria. This is the first report of its occurrence on *L. coriaceum*, but no attempt has been made to test its pathogenicity.

Thus, despite the loss of many above-ground shoots and the death from unknown causes of a significant number of the frost-induced coppice shoots, the vegetative regenerative potential of this species appears to be intact, though some sites, (e.g. site 6) lost the majority of their adult shoots.

Footnote 5 of Table 8 notes that seedling numbers in 900 m² quadrats in each site were low and variable. Cheal *et al.* (1979) state that the immediate post-fire responses of this species are unclear, but list the plant as a facultative root resprouter. Specht (1981) states that

seedling regeneration in heath vegetation in southern Australia is limited to the period immediately after fire and again when gaps begin to occur in the mature and senescent phases 25 to 50 years post-fire. His data show that the closely-related coastal teatree, *L. laevigatum*, consisted entirely of a population of seedlings at Wilson's Promontory. Unpublished observations in other areas of Wyperfeld regenerating after fires in 1977 suggest that seedlings are an important source of post-fire regeneration in this species. Unlike the eucalypts, seed viability of this species does appear to be affected by severe freezing treatments (see Tables 4 and 5). The results are complex and hard to interpret. Thus, at Eastern Lookout, seeds from green capsules give a higher result in all treatments than seeds from brown capsules, whereas the reverse is true for seeds from capsules from Flagstaff Hill. This produced the unusual result that overall, capsule colour showed no significant effects, but did show a highly significant interaction with locality. Locality also affected the impact of a second freezing period. Seed extracted from capsules at Eastern Lookout showed an extra reduction in mean viability with a second freezing treatment while that from Flagstaff Hill, which has a significantly lower viability after the first treatment, does not show the same response. Further study of multiple-freezing treatments is needed to evaluate the effects of successive treatments for this species.

The intact plants frozen in the field had turned brown and shed seeds from frozen capsules 4 days after the treatment. Given this rapid response, it seems likely that severe frosts would have induced a fairly massive seed release in this species. Even if a majority of seeds were rendered inviable, the low and variable numbers of seedlings re-establishing in the frosted areas seems too low to be due to the impact of frost *per se*. It will be most interesting to assess the belt transect installed in February 1985 at Meridian Track in an area severely frosted in 1982 and then burnt in January 1985. As with the *B. ornata*, such an area will give an interesting comparison with areas re-establishing after fires that were not preceded by frosts.

The Mallee Eucalypts

After a fire, coppice shoots arise chiefly from the lignotuber as it is rare for above ground foliage to survive (Cheal *et al.* 1979). After the 1982 frost, these species also produced coppice but in a pattern that reflected the severity of the frost kill. Severely-affected trees died back to or close to ground level and coppiced from the basal stem or lignotuber, while less severely-affected trees coppiced along the length of the aerial stems.

Very few seedlings were found along the belt transect at Nine Mile Square Track, dramatically fewer (6 vs 169) than those induced by the fire of 1981 along half the length of transect at Ginap Track. Seedling frequency is not consistently related to the degree of frost severity of the parent tree (see Table 9), though those data confirm the low seedling frequency found in the belt transect. It

was thought at first that the frosts may have killed seeds within the capsules, but the data of Table 6 and 7 show that this is highly unlikely: dry seeds exposed to 7 successive cycles at -20°C , are quite resistant—only germinated seed is susceptible.

Wellington (1984) and Wellington and Noble (1985a, b) have shown that the establishment of seedlings in long unburnt stands of *E. incrassata* is limited by ant predation of the low rate of seed input, and by adult competition for nutrients and water. After fire there is a dramatic increase in the rate of seed input, and sharp reduction in the competitive power of the adults, especially for water. Between them, these factors lead to the establishment of high numbers of seedlings in the early years after a fire. If it is assumed that frozen capsules open in the field (capsules removed from trees and experimentally frozen and thawed opened in a few days at 30°C), one would expect a massive seed release in severely frosted areas, a period of reduced adult competition, and the establishment of a large population of seedlings. Unfortunately, measurements were made only at Nine Mile Square Traek and did not begin till early in 1985, two and a half years after the frosts, so it is not possible to be sure exactly what happened immediately after the frosts. However, casual observations were made in August 1983 and August 1984 in several locations in the Park and large seedling populations were never sighted in frost-killed areas. Perhaps seed release, after frost kill in winter, does not generate the sudden massive seed input that follows fires in summer and the ants are able to harvest most of the frost-induced seed fall. Although other interpretations are possible, the total absence of seedlings from the litter layer around frost-damaged trees (see Table 9) could be interpreted to support this view in that chance burial of seed by wind-movement of sand or passing animals might be easier in the litter-free zone. Alternatively, frost-induced litter may have an inhibitory effect upon germination or establishment of mallee eucalypt seeds. With difficulty, it would be possible to test some of these points by using the portable freezer to freeze small samples of eucalypts in the field. Certainly, the conditions surrounding the establishment of seed after a severe winter frost and a prolonged drought are likely to be different from those after summer fires followed by autumn rains.

CONCLUSIONS

The severe frosts of 1982, perhaps interacting with the ensuing drought, had dramatic immediate effects on *B. ornata*, *L. coriaceum* and the mallee eucalypts. With the exception of sporadic survivors, all adult *B. ornata* in frost-affected swales were eliminated. Field-grown seedling *B. ornata* appears to be highly resistant both in areas exposed to field frost, and when tissues were tested by very severe experimental freezing treatments. The seed in the cones in the frost-killed areas is still viable, based on the tetrazolium test, but it is not germinable and seedlings are rare in frost-killed areas at present (latest observations April 1986). Fire in 1985 burnt a

large stand of frost-killed *Banksia* near Meridian Traek (site 10, Fig. 1), but this area has regenerated very few seedlings also (less than 1 survivor/1000 m^2 in a large fixed quadrat of 4500 m^2).

L. coriaceum showed high and variable kills of standing foliage, but even in areas that showed 100% loss of leaves and up to 80% loss of mature stems, the population is recovering by coppicing and suckering. Seedling regeneration is weak and variable with site and there is some evidence that seed of this species may be damaged in the capsules by repeated exposure to severe freezing temperatures.

The mallee eucalypts respond to frost damage by coppicing, in a pattern related to the severity of the damage. Only a very small number of seedlings have established in the frost-killed areas, the majority of which lie in bare ground outside the litter layer.

We conclude that *B. ornata* has suffered serious damage from the winter of 1982 and the ensuing drought. Such severe conditions may provide a limitation to the distribution of *B. ornata* over long periods of time, similar perhaps to the influences of frost on distributions of eucalypts in subalpine Tasmania reported by Davidson and Reid (1985). *L. coriaceum* and the mallee eucalypts are recovering strongly.

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OBSERVATIONS ON THE ECOLOGY OF *GALAXIELLA PUSILLA* (MACK) (SALMONIFORMES: GALAXIIDAE) IN DIAMOND CREEK, VICTORIA

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ABSTRACT: Aspects of the life history and diet of the dwarf galaxiid, *Galaxiella pusilla*, in Diamond Creek, southern Victoria, were studied between March 1983 and February 1984. *Galaxiella pusilla* inhabited the slow-flowing creek during the dry months of the year and moved to an adjacent swamp in early winter. Spawning occurred in late winter and early spring, when males possessed a mean G.S.R. of 9.8 and females a G.S.R. of 16.4. The diameter of the eggs of ripe females varied between 0.8 and 1.0 mm and the number of eggs per female varied between 66 and 247. Only one age class was found, suggesting that *Galaxiella pusilla* is an annual species. Length-weight analysis showed no deviation from isometric growth. *Galaxiella pusilla* is a generalist carnivore.

The genus *Galaxiella* McDowall includes the smallest representatives of the family Galaxiidae. Three species are currently recognised (McDowall 1978): *Galaxiella nigrostriata* (Shipway) and *Galaxiella nunda* McDowall, both of which occur only in Western Australia, and *Galaxiella pusilla* (Mack) which is found in southern Victoria, on Flinders Island and in north-eastern Tasmania (McDowall & Frankenberg 1981).

Whilst some taxonomic studies and accounts of the distribution have been published (see McDowall & Frankenberg 1981, Cadwallader & Backhouse 1983), little is known about the biology of *G. pusilla*, although observations of the spawning behaviour in aquaria have been reported (Backhouse & Vanner 1978). The secretive nature of the fish and its characteristically small populations may account for this lack of attention. This study is an account of the growth, development, reproduction and diet of *G. pusilla* from one locality in Victoria.

METHODS

Galaxiella pusilla was collected monthly from Diamond Creek, 5 km south-east of Tonimbuk, Victoria. Diamond Creek is a tributary of the Bunyip River which it joins about 1 km downstream from the collecting site.

During the summers of 1982-83 and 1983-84 the creek at the collecting site flowed in a narrow channel up to 6 m wide. However, during the intervening wet period the creek overflowed into an adjacent swamp (a regular occurrence) and water covered an area of about 2 ha to a maximum depth of 1.5 m. While the swamp was dry, sampling was conducted only in the creek proper, but when the swamp filled, both the creek and the swamp were sampled.

Fish were collected using a long-handled dip-net with a 1 mm mesh and a 210 × 250 mm mouth. Fish were preserved immediately in 10% buffered formalin and

within 24 h of collection were wet weighed to the nearest 10 mg and their total lengths (TL) measured to 0.1 mm with vernier calipers.

The gonads of *G. pusilla* were observed and staged according to a scheme modified from Pollard (1972). Gonads were classed in six stages rather than seven as Pollard (1972) used. The six stages were: 1—not developing; 2—developing; 3—maturing; 4—mature; 5—ripe; and, 6—spent. Gonads of sexed fish were removed and weighed. The weight was expressed as a percentage of the total weight of the fish: the gonadosomatic ratio or G.S.R. The diameters of thirty eggs from each ripe female were measured and the eggs from eight mature and ripe females were counted to determine fecundity. The stomach contents of 48 *G. pusilla* were analysed by the numbers method (Hynes 1950) from samples collected between March and September 1983.

RESULTS

HABITAT

When collected from the creek proper, *G. pusilla* as well as the southern pigmy perch, *Nannoperca australis* Günther, were commonly found amongst emergent bank-side vegetation. When the adjacent swamp filled, the two species were found associated with both submerged and emergent vegetation. Larval *G. pusilla* preferred open water although, when disturbed, they invariably took shelter in submerged vegetation.

SEX RATIO

Of the 158 *G. pusilla* collected, 73 were adults; the remainder were larvae and juveniles. Of the 73 adults, 28 were males and 45 were females. The sex ratio was 1:1.6 which does not differ significantly from 1:1 ($X^2 = 3.96$, $df = 1$, $p > 0.05$).

LENGTH-FREQUENCY ANALYSIS

Only one age class of *G. pusilla* was observed until the first juveniles were recruited into the population in August 1983 (Fig. 1). The fish increased in size from March until June, when growth ceased. Fish were first collected from the swamp in July (when the swamp first filled) and these individuals were found, on average, to be significantly smaller than in the previous month ($t = 4.94$, $df = 14$, $p = 0.0001$). Growth then resumed until September, after which no adults were found. Larvae were first collected in August and these increased in size until January 1984. At this time, the swamp dried up and fish were collected from the creek proper again.

LENGTH-WEIGHT RELATIONSHIPS

The 'b' values, indicating condition of the fish (Le Cren 1951), proved not to be significantly different from the isometric value of 3 (Table 1). Males and females were

compared by an analysis of covariance (Zar 1974) performed on the linear log-log plots to test for differences between slopes and between elevations. There was no significant difference between slopes ($F_{1,44} = 0.8800$) or between elevations ($F_{1,45} = 1.6306$).

GONADAL DEVELOPMENT

Stages of Maturation

The sexes of the fish were distinguishable and the gonads had begun developing by the time the fish were between 3 and 4 months old (Fig. 2). When the fish were about 9 months old the majority had gonads at Stage 3 and could be sexed by eye. At Stage 4 the ovaries clearly distended the body wall, while the testes had not yet filled the body cavity. When both sexes were ripe (Stage 5) the females were considerably distended and the males possessed testes that filled the body cavity.

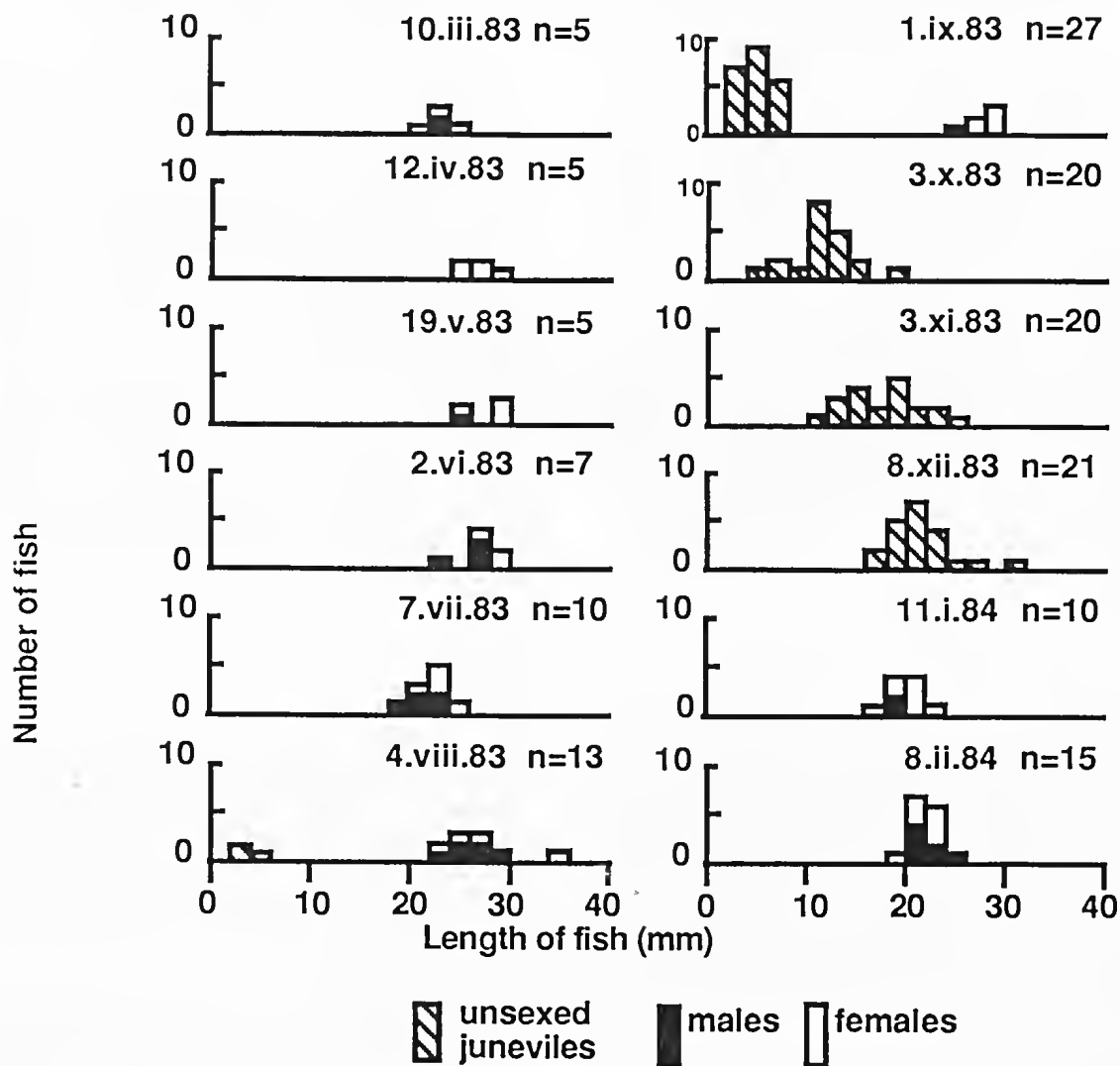


Fig. 1 — Length-frequency distributions for *G. pusilla*, collected at monthly intervals in Diamond Creek, Victoria.

TABLE 1

LINEAR MODEL OF LENGTH-WEIGHT REGRESSIONS FOR MALE, FEMALE AND TOTAL *G. pusilla* OF THE FORM $\log W = \log a + b \log L$; VALUES OF b WERE NOT SIGNIFICANTLY DIFFERENT FROM 3.00 ($0.1 > p > 0.05$).

	N	a	b	F ratio	r ²
Males	28	0.83	3.05	107.65	0.81
Females	45	0.72	3.41	341.16	0.89
Total	73	0.73	3.36	465.55	0.87

In August the first ripe fish were collected from the swamp and the first larvae (represented by Stage 1 fish) were found. The absence of Stage 6 (spent) fish indicates either the death of fish after spawning or an emigration of all spent adults.

Gonadosomatic Ratios

The mean monthly gonadosomatic ratios for sexed *G. pusilla* are shown in Table 2. Not until May (when the fish were 8-9 months old), did the G.S.R.'s of the sexes differ substantially from each other. From May to September, in most instances, the ovaries contributed more to the weight of the female than the testes did to the weight of the male. In June, one male had an extraordinarily high G.S.R. of about 30 (all other males possessed gonads not in excess of 12), and this was the reason for the high mean G.S.R. attributed to males for that month. If this single specimen is excluded from analyses, the G.S.R.'s of both sexes peaked in August, at 9.8 for males and 16.4 for females.

TABLE 2

GONADOSOMATIC RATIOS FOR *G. pusilla* * = none in sample; † = GONADS OF JUVENILES TOO SMALL TO WEIGH (N) = NUMBER IN SAMPLE

Date	Male	Female
10. iii. 1983	0.97 (2)	0.93 (3)
12. iv. 1983	*	2.19 (5)
9. v. 1983	3.55 (1)	4.41 (4)
2. vi. 1983	12.28 (4)	10.92 (3)
7. vii. 1983	3.21 (5)	5.91 (5)
4. viii. 1983	9.84 (6)	16.44 (4)
1. ix. 1983	6.69 (1)	16.40 (5)
3. x. 1983	†	†
3. xi. 1983	†	†
8. xii. 1983	†	†
11. i. 1984	0.73 (2)	0.66 (8)
8. ii. 1984	0.70 (7)	0.94 (8)

Eggs and Fecundity

Ripe females possessed oocytes between 0.8 mm and 1.0 mm in diameter. Egg numbers varied between 66 and 247 (mean 150) per fish (TL range 23.7-36.3 mm). The relationship between fecundity of mature and ripe females can be described by the equation $F = 0.0044L^{3.0516}$, where F = fecundity, and L = length of fish ($r^2 = 0.8770$, $F = 43.1330$).

The adhesive eggs were deposited singly upon stems of emergent macrophytes within the swamp.

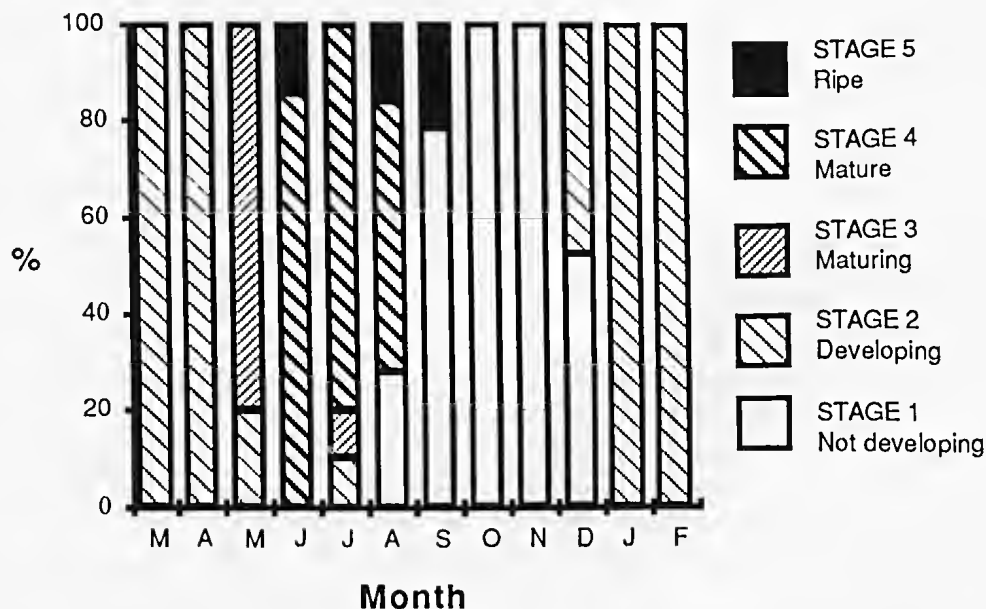


Fig. 2—Gonadal maturation stages for *G. pusilla* collected in Diamond Creek, between March 1983 and February 1984; sample sizes as in Figure 1 (male and female data pooled).

DIET

G. pusilla predominantly ate planktonic crustaceans, although chironomid larvae were often present in the stomachs in large numbers (Table 3).

When the fish first inhabited the creek proper, chydorid eladocerans and cyclopoid copepods were the dominant components of the diet, whereas daphniid eladocerans and harpacticoid copepods were present in large numbers in the stomachs of fish collected from the swamp. Ceratopogonids and collembolans were eaten in four months of the study, while terrestrial insects were eaten in most months and, although they were not taken in large numbers, the volume of each food item was considerable.

TABLE 3
DIET OF *G. pusilla* (N=48) COLLECTED IN DIAMOND CREEK BETWEEN MARCH AND SEPTEMBER 1983.

Food item	No. of items	% of total items
DIPTERA		
Chironomidae (larvae)	200	5.2
Ceratopogonidae (larvae)	17	0.4
HEMIPTERA (adult)	1	<0.01
COLEOPTERA (larvae)	2	<0.01
TERRESTRIAL INSECTA	40	1.0
COPEPODA		
Cyclopoida	779	20.2
Harpacticoida	971	25.2
Calanoida	71	1.8
CLADOCERA		
Chydoridae	690	17.9
Daphniidae	427	11.1
OSTRACODA	479	12.4
CRUSTACEA (larvae)	11	0.3
COLLEMBOLA	137	3.6
HYDRACARINA	2	<0.01
TERRESTRIAL ARANEAE	2	<0.01
UNIDENTIFIED	19	0.5

DISCUSSION

Galaxiella pusilla typically inhabits slow-flowing or still water bodies, such as creeks, drains and swamps. It is sometimes found in temporary waters and its continual reappearance in these habitats has led some authors to suggest that aestivation is used as a survival strategy (McDowall & Frankenberg 1981). The aestivating abilities of *Neochanna apoda* Günther and *N. burrowsius* (Phillips) have been well documented (Eldon 1978, 1979) and there is evidence to suggest that *Galaxias cleaveri* Scott can also aestivate (McDowall & Frankenberg 1981). However, the suggestion that the survival of *G. pusilla* during dry conditions involves desiccation-resistant eggs (McDowall & Frankenberg 1981) appears unlikely because of the timing of reproduction. In Diamond Creek, the fish spawned in late winter and early spring, the eggs hatched and the

young were at least four months old before the swamp dried up. In the present study, all growth parameters (length, weight, maturation stages, egg size and G.S.R.) showed similar patterns of development: increase between March and June, a check in July, followed by a further increase leading up to maturity and spawning. The reason for this apparent check is unclear, but may be a function of small sample sizes and the fact that sampling was necessarily shifted to the swamp in July.

Female *G. pusilla* usually attain a maximum G.S.R. considerably greater than that of males, in common with *Galaxias vulgaris* Stokell, *G. maculatus* (Jenyns), *G. fasciatus* Gray and *Neochanna apoda* (see Cadwallader 1976, Pollard 1971, Hopkins 1979, Eldon 1979). *G. pusilla* spawns at the same time as most totally freshwater galaxiids (Campos 1972, McDowall & Frankenberg 1981, Fulton 1982). Conditions were favourable for spawning in Diamond Creek in late winter and early spring; the swamp was full and the aquatic vegetation luxuriant so that food resources were abundant and ample sites existed for the deposition of eggs. The size of eggs collected from ripe female *G. pusilla* was typical of non-migratory, freshwater galaxiids. Generally those galaxiids which migrate to estuaries or the sea as part of their life histories are thought to possess numerous small eggs, while those which spend their entire life in freshwater usually have a smaller number of large eggs (Benzie 1968, McDowall 1970).

It is suggested here that *G. pusilla* is an annual species, the adults dying after spawning. The samples collected indicate the presence of only one year class, although in August and September overlaps between one generation and another occurred as some adults had not yet spawned at a time when juveniles were already being recruited into the population. *G. pusilla* attains its maximum size within a year of hatching (unlike many other galaxiids which may take several years to complete growth) and aquarium observations indicate that *G. pusilla* die after spawning (Massola 1938, pers. obs.). If *G. pusilla* is an annual species, it may be unique among galaxiids, although *G. nigrostriata* and *G. munda* have not been studied sufficiently to draw any conclusions regarding their longevity. A large percentage of *Galaxias maculatus* are thought to die at the end of their first year, after spawning, however, some do survive and spawn in the following year (Pollard 1971).

G. pusilla is a generalist carnivore, which feeds mainly in the water column on zooplankton. Throughout the study, planktonic crustaceans and chironomids were the major food sources. These two food types were present in large numbers both in the creek and the swamp. The diet of *G. pusilla* is similar to those of other galaxiids which inhabit still or slow-flowing water bodies (McDowall & Frankenberg 1981). Backhouse and Vanner (1978) suggested that algae is a constituent of the diet of *G. pusilla* in aquaria. However, this did not appear to be the case in the present study. Furthermore, algae never constituted a part of the diet of wild fish even though it was abundant in many forms in the habitat.

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DISTRIBUTION OF VASCULAR HYDROPHYTES AND DESCRIPTION OF ASSOCIATED MACROFAUNAL COMMUNITIES IN SWAN BAY, VICTORIA

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ABSTRACT: The biomass of vascular hydrophytes in Swan Bay was measured at fifty sites. Macrofaunal distribution was examined at eleven intertidal sites. Five species of vascular hydrophyte were collected: *Heterozostera tasmanica*, *Zostera muelleri*, *Halophila ovalis*, *Lepilaena cylindrocarpa* and *Ruppia megacarpa*. The dominant species was *H. tasmanica* which was found at 90% of the sites and had a mean standing crop of 104 g dry weight m⁻². *Z. muelleri* and *L. cylindrocarpa* were restricted to the intertidal zone. *H. ovalis* was found only at subtidal sites and *R. megacarpa* was found only rarely. A total of 74 taxa of invertebrates was taken, the majority of which were detritivores (75%). Hierarchical analysis showed differences between sites covered with vascular hydrophytes and sites only sparsely covered. Fewer species were found associated with the latter sites. Community statistics were similar to those of other Australian seagrass communities. However, species composition of the Swan Bay community differed from other *H. tasmanica*-*Z. muelleri* communities, indicating that there is no 'typical' *H. tasmanica*-*Z. muelleri* benthic macrofaunal community.

While details of the distribution of various species of seagrass around the coast of Australia have been published (den Hartog 1970, McComb *et al.* 1981), little quantitative information is available on the invertebrate communities that these seagrasses support. Hutchings (1982) has reviewed the literature on the fauna of Australian seagrass ecosystems and, more recently, quantitative studies of the fauna of *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog and *Zostera muelleri* Irmisch ex Aschers. communities in Westernport Bay, Victoria (Watson *et al.* 1984) and *Posidonia australis* Hook. f. communities along the coast of New South Wales (Collett *et al.* 1984) have been published.

This paper reports the distribution of seagrasses and other vascular hydrophytes in Swan Bay, Victoria, and some aspects of the associated fauna. Faunal studies concentrated on intertidal and shallowly-subtidal animal communities. A preliminary description of the seagrasses of Swan Bay has been published (Kerr 1982) but this is the first account to present quantitative information on the distribution of the seagrasses and their associated macrofauna in the Port Phillip Bay region.

Swan Bay (38° 14'S, 144° 40'E) is a shallow, soft-bottom embayment, with an area of approximately 3000 ha (Figs 1A, B). The sediments are clayey sands with shell fragments constituting nearly all the sand-sized particles (Beasley 1966). A major feature of the bay is an extensive series of intertidal mudbanks (Fig. 1B). Exchange with Port Phillip is limited to two navigable channels, a dredged channel south of Swan Island and a northern channel. Surface drainage of the catchment area on the western side of Swan Bay is confined to intermittently flowing creeks.

METHODS

Ten samples, each of 0.025 m² area, of vascular hydrophytes were taken from each of fifty sites during July-December 1978. The sites (Fig. 2) were randomly selected from an original grid of 500 such sites. Each site covered an area of approximately 6 ha and the position of samples within each site was determined by using random number tables. A quadrat was used to mark each sample and all plant material within this quadrat to a depth of 8-10 cm was collected. Samples were sorted and angiosperm species identified. Above and below ground parts were not separated. After rinsing in 5% phosphoric acid to remove epiphytes, the sorted samples were dried to constant weight and dry weights were determined.

Samples of benthic macrofauna were taken from eleven sites during May-August 1978. Sites (Fig. 2) were selected from intertidal areas of heavy seagrass growth. For comparison, two areas of sparse plant cover were also sampled. At each site, either six or ten random samples were taken from a marked 30 m square using a spade corer (area = 0.03 m²). Samples were washed on a 1 mm mesh sieve and preserved in 5% formalin-seawater solution. Samples were sorted and invertebrates were identified to the lowest possible taxonomic level and counted. For each site a number of community statistics were calculated: S, the total number of taxa per site; s, the number of taxa per sample; n, the mean number of individuals per sample; H', the Shannon-Weaver diversity index (to the base e); and, J', the evenness. For heavily-grassed sites, N, the total abundance of invertebrate taxa (No. m⁻²) also was calculated.

Hierarchical analysis was used to compare all sites. Two indices, Czekanowski's formula of faunal affinity

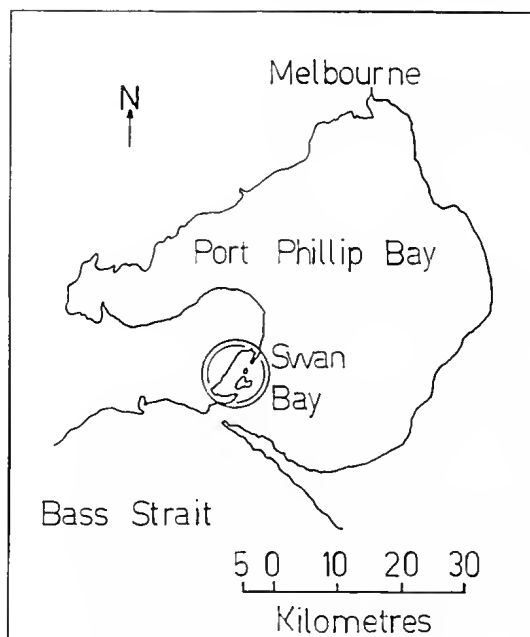


Fig. 1A—The general location of Swan Bay

and the Canberra metric coefficient of dissimilarity were used. The first index takes account of presence/absence data only, while the second also takes account of the numbers of each taxon present. A group averaging strategy was used to fuse the sites (Clifford & Stephenson 1975). Using the literature and observations in the field, taxa were assigned to feeding types: herbivores, omnivores, predators, scavengers, suspension feeders, unspecified or detritivores. The term 'detritivore' is used to include both sediment-ingesting deposit feeders and those organisms that consume larger detrital particles.

RESULTS

Five species of vascular hydrophytes were collected: *Zostera muelleri*, *Heterozostera tasmanica*, *Halophila ovalis* (R.Br.) Hook. f., *Lepilaena cylindrocarpa* (Kocernicke ex Walp.) Benth. and *Ruppia megacarpa* Mason. The dominant species in terms of biomass and the most wide-ranging was *H. tasmanica* which occurred in intertidal and subtidal zones (Table 1, Fig. 3). At many of the subtidal sites it was the only species found. The next most common species, *Z. muelleri*, was restricted to intertidal or shallowly-subtidal sites (Table 1, Fig. 3). It was found in association with *L. cylindrocarpa* in areas of greatest exposure (Fig. 3). *L. cylindrocarpa* was also found in monospecific stands in the pools and watercourses on the northern and western sides of the bay. *H. ovalis* (Table 1, Fig. 3) was found only at the deeper northern sites in association with *H. tasmanica*, and at sites 27, 29, 30, 33 and 36 was present in greater abundance than *H. tasmanica*. *R. megacarpa* was found in the Yarram Creek area and growing in the creek itself, but was not found at any of the sampling sites.

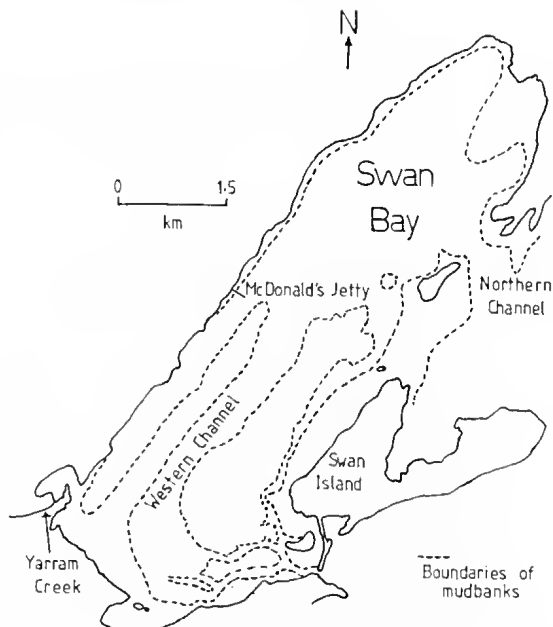


Fig. 1B—Location of mudbanks, channels and other features of Swan Bay.

A total of 74 taxa of invertebrates was recorded. Of these, 39% were polychaetes, 35% crustaceans and 18% molluscs. The ten most common taxa accounted for nearly 80% of animals taken (Table 2). Detritivores dominated both number of taxa and individuals (Table 3). Diversities and numbers of taxa were lower at

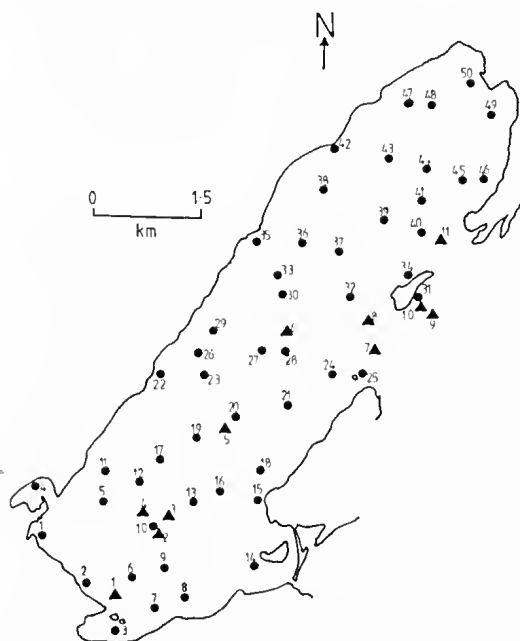


Fig. 2—Sampling points for survey of vascular hydrophytes (●) and invertebrates (▲) within Swan Bay.

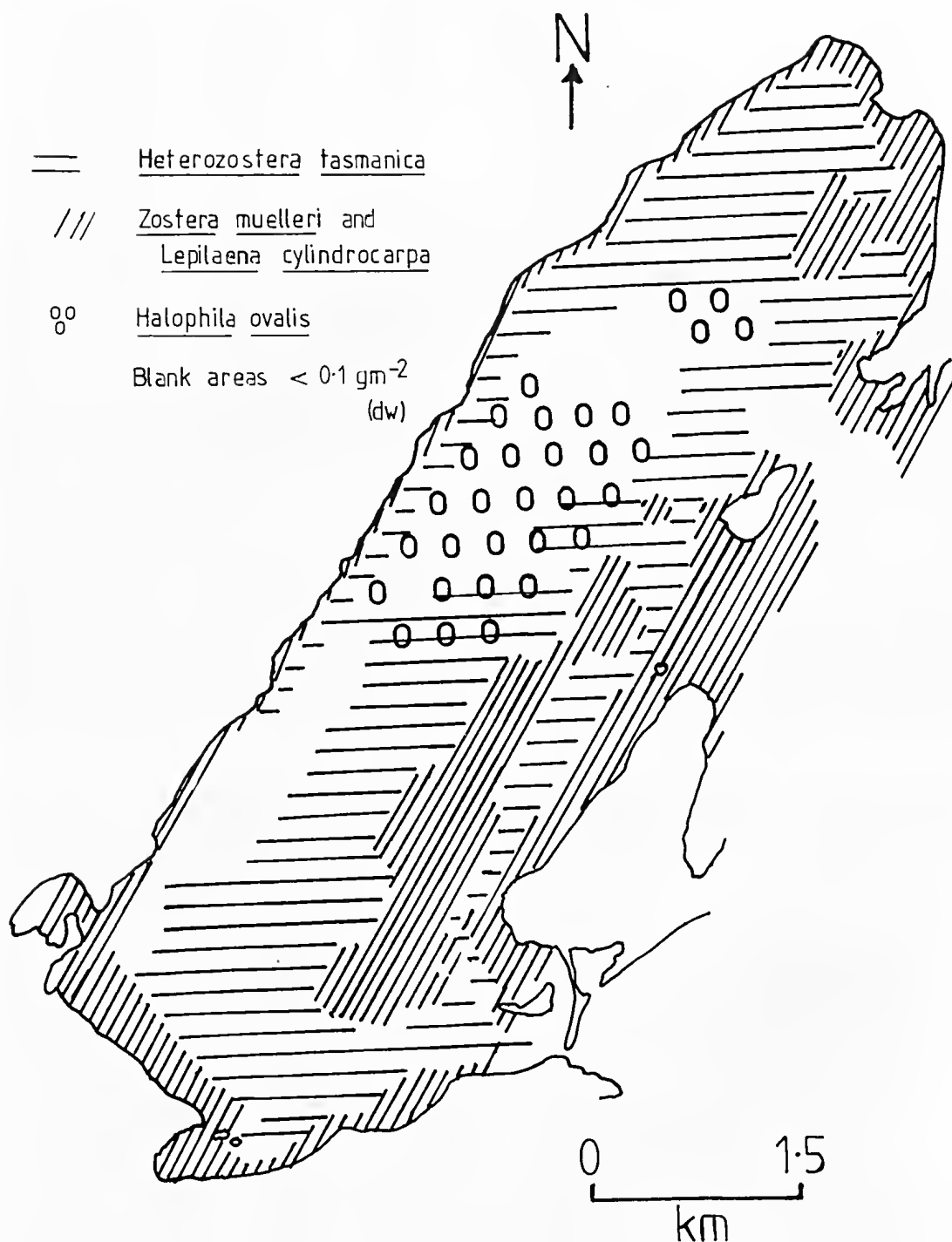


Fig. 3—Distribution of vascular hydrophytes within Swan Bay

TABLE 1
BIOMASS AND DISTRIBUTION OF VASCULAR HYDROPHYTES

Species	Mean dry weight (g m ⁻²)	Upper limit (g m ⁻²)	% of total dry weight	% of sites at which found
<i>Heterozostera tasmanica</i>	103.5	405	73.8	90
<i>Zostera muelleri</i>	44.2	151	15.4	44
<i>Lepilaena cylindrocarpa</i>	16.4	71	5.7	36
<i>Halophila ovalis</i>	15.4	66	3.1	22

ungrassed sites, while the number of individuals per sample was higher at these sites (Table 4).

Hierarchical analysis reflected the differences in community statistics. Both indices fused the sites into two groups, one comprising the two sparsely-grassed sites, the other formed by the heavily-grassed sites (Figs 4A, B). The similarity of the results from both indices indicates that both species composition and numbers contributed to the differences between the two groups of sites. No major differences were shown between the heavily-grassed sites indicating the general evenness of the intertidal seagrass community of Swan Bay.

DISCUSSION

This study provides quantitative data on the biomass of vascular hydrophytes from an area within Port Phillip Bay. It supports the qualitative work of Bulthuis (1981a) which showed that in almost all areas of the bay where vascular hydrophytes grow, *H. tasmanica* was the

major species. Bulthuis (1981b) has reported biomass data for *H. tasmanica* in Westernport Bay. However, the samples were taken in summer (compared with winter/spring in this study) and the sampling procedures were different.

The intertidal vascular hydrophytes of Swan Bay support a polychaete-erustacean-mollusc community dominated by detritivores. This dependence on the detrital pathway is a feature of temperate seagrass beds (Kikuehi 1980). There were differences between heavily-grassed and sparsely-grassed sites within Swan Bay; the latter showed either marked decreases in the abundance or complete absence of many of the commoner infaunal species. Similar depauperation of the infauna has been shown in other seagrass communities: *Z. marina* L. (Orth 1973), *Z. capricorni* Aschers. (Hutchings & Recher 1974, Hutchings *et al.* 1978, Rainer & Fitzhardinge 1981). All these authors found higher diversities and abundances in seagrasses than in nearby bare sediment. The higher total densities at ungrassed sites in Swan Bay were mainly due to the

TABLE 2
TAXA FROM TOTAL SAMPLE RANKED BY NUMBER OF INDIVIDUALS
Key to taxa: C = Crustacean; P = Polychaete; and, M = Mollusc

Species	Number	Cumulative %	Taxa
<i>Allorchestes compressa</i>	2846	21.3	C
<i>Capitella capitata</i>	2300	34.1	P
<i>Zeacumantus diemenensis</i>	1516	42.5	M
<i>Paracorphium</i> sp.	1441	50.5	C
<i>Ceratonereis pseudoerythraensis</i>	1140	56.8	P
<i>Scoloplos cylindrifer</i>	1094	62.8	P
<i>Heteromastus filiformis</i>	872	67.9	P
<i>Leptochelia ignota</i>	761	71.9	C
<i>Corophium</i> sp.	702	75.8	C
<i>Austrocochlea constricta porcata</i>	511	78.6	M
<i>Amphithoe</i> sp.	478	82.3	C
<i>Armandia intermedia</i>	335	83.1	P
<i>Paracallioppe australis</i>	332	85.0	C
<i>Tellina deltoidalis</i>	328	86.8	M
<i>Nemertean</i> s, unidentified	328	88.3	
<i>Brachynotus spinosus</i>	178	89.3	C
<i>Platynympha longicauda</i>	156	90.2	C
<i>Amarinus laevis</i>	140	90.9	C
<i>Anthozoan</i> sp. 1	124	91.6	
<i>Prionospio multipinnulata</i>	116	92.3	P

TABLE 3

NUMBER AND PERCENTAGES OF TAXA AND INDIVIDUALS IN VARIOUS FEEDING GROUPS. s = number of taxa,
n = number of individuals

Trophic group	s	%s	n	%n
Herbivore	5	6.4	632	3.5
Detritivore	34	43.6	13559	74.4
Predator	18	23.1	785	4.3
Omnivore	7	9.0	1496	8.2
Scavenger	4	5.1	159	0.9
Suspension feeder	6	7.7	1489	8.2
Unspecified	4	5.1	108	0.6

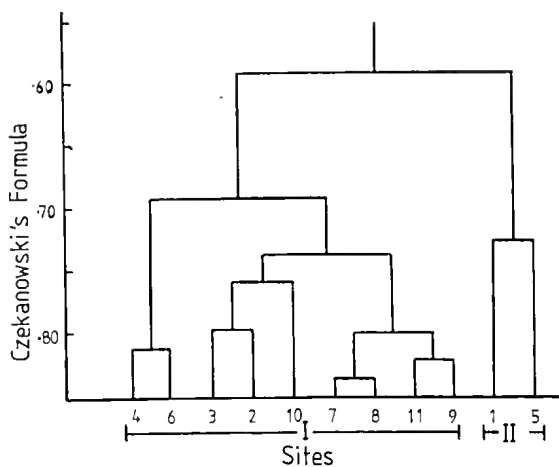


Fig. 4A—Invertebrate sampling sites grouped by hierarchical classification using Czekanowski's formula.

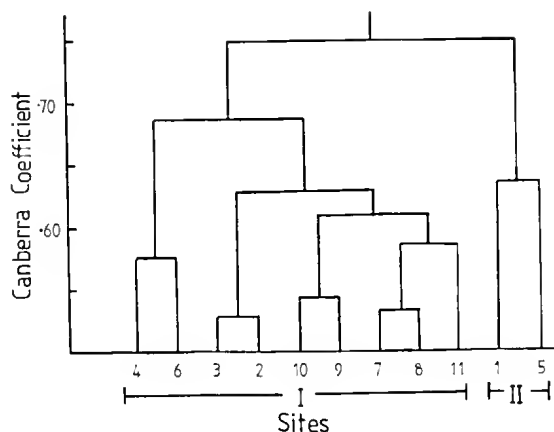


Fig. 4B—Invertebrate sampling sites grouped by hierarchical classification using the Canberra metric coefficient.

TABLE 4

COMMUNITY STATISTICS FOR BENTHIC SITES. Sparsely grassed sites marked with an asterisk (*). See text for explanation of symbols.

Site	H'	J'	S	s	n
1*	2.15	0.65	28	15.8	227.5
2	2.46	0.68	38	21.8	148.6
3	2.21	0.60	39	19.5	142.0
4	2.63	0.70	43	24.0	143.5
5*	2.07	0.62	28	16.0	302.3
6	2.61	0.72	37	20.6	95.0
7	2.32	0.63	40	22.0	221.7
8	2.56	0.67	47	32.9	220.3
9	2.34	0.61	47	22.8	197.4
10	2.32	0.68	31	20.5	122.0
11	2.56	0.64	55	27.2	216.5

$$H' = 2.38 \pm 0.18 \quad J' = 0.65 \pm 0.04 \quad S = 39 \pm 8$$

TABLE 5
COMPARISON OF COMMUNITY STATISTICS FOR A RANGE OF AUSTRALIAN SEAGRASS COMMUNITIES.
SEE TEXT FOR EXPLANATION OF SYMBOLS

Authors	Site	Seagrass	H'	J'	S	N
Rainer & Fitzhardinge (1981)	Cabbage Tree Basin N.S.W.	<i>Z. capricorni</i>	1.31	0.46	87	8760
Poore (1982)	Gippsland Lakes (Site 13)	<i>P. australis</i>	1.99	0.73	94	2780
Watson <i>et al.</i> (1984)	Westernport Bay	<i>Z. muelleri</i>	2.45	0.76	54	20-25,000
Collett <i>et al.</i> (1984)	(a) Crib Point	<i>Z. muelleri</i> & <i>H. tasmanica</i>	2.91*	—	56	2097
	(b) Rhyll	<i>Z. muelleri</i> & <i>H. tasmanica</i>	2.93†	—	72	1984
	Forster (NSW)	<i>P. australis</i>	3.95	—	39	597
	Shoal Bay	<i>P. australis</i>	4.67	—	100	4629
Present study	Swan Bay	<i>Z. muelleri</i>	2.45†	0.66	74	5437‡
		<i>H. tasmanica</i>				
		<i>L. cylindrocarpa</i>				

* mean of two transects (24 sites); † mean of one transect (12 sites); ‡ mean of 9 sites

presence of large numbers of a few species of opportunistic crustaceans (including *Corophium* sp. and *Paracorophium* sp., Dorsey 1982). These two species are subject to irregular population fluctuations and are not a consistent component of the benthic fauna.

A number of the common species in Swan Bay are considered to be estuarine and are prevalent in other parts of Port Phillip Bay (Poore & Kudenov 1978a, b). These include *Scoloplos cylindrifer*, *Corophium* sp. and *Amarinus laevis*. Some of the other common species have been recorded from estuarine areas on the south-eastern coast of Australia including *Tellina deltoidalis* and *Armandia intermedia* (Hutchings *et al.* 1978, Rainer & Fitzhardinge 1981, Poore 1982). A number of the estuarine species found in Swan Bay (*Capitella capitata*, *Corophium* sp.) are opportunistic (Dorsey 1982, Grassle & Grassle 1974) and so are able to take advantage of changed conditions.

Swan Bay shows both structural similarities to and differences from seagrass communities studied elsewhere in Australia. The proportion of taxa in each trophic level is similar to those reported in beds of *Posidonia australis* in N.S.W. (Collett *et al.* 1984) and *Z. capricorni* in an estuary in N.S.W. (Rainer & Fitzhardinge 1981). Community statistics were also used to compare the Swan Bay community to other Australian seagrass communities. Differences in sampling methods and sampling intensities make comparison of community abundance and diversity statistics difficult (Rainer & Fitzhardinge 1981). However, some general trends can be indicated by such comparisons. Table 5 lists community statistics for a number of south-eastern Australian seagrass communities. Diversities ranged from a low of 1.31 in the estuarine Cabbage Tree Basin to a high of 4.67 in a marine *Posidonia* meadow at Shoal Bay. The diversity for Swan Bay falls mid-way between these values and is comparable to the values for other Victorian sites. Species abundances varied greatly between sites with Swan Bay again in the mid-region for these values, as with the number of species found at each site. In terms of community structure, as shown by a number of community statistics, Swan Bay supports a moderately-diverse macrobenthic community comparable in structure to other such communities in southeastern Australia.

Despite the similarities in trophic and community structure, the species composition of the Swan Bay benthic community is different from those of the other communities mentioned above. Many of the species found in Swan Bay are either missing or found only rarely at the other sites. Hutchings (1982) noted the lack of 'characteristic' seagrass communities so far described in Australia. In a study of *Posidonia* meadows in N.S.W. (Collett *et al.* 1984), different sites were found to support communities of differing species. These compositional differences were thought to be mainly due to salinity differences between sites. Rainer and Fitzhardinge (1981), reviewing the faunal communities of estuarine *Z. capricorni* beds in N.S.W., found that a number of species were common to different sites but that dominant species varied from site to site. The community of *H. tasmanica* and *Z. muelleri* beds in Westernport Bay

described by Watson *et al.* (1984) has a range of species that are also found in Swan Bay, but the dominant species were different. Two of the dominant species in Westernport Bay (*Nephtys* and *Callinassa*) were not taken from Swan Bay. Similarly a *Z. muelleri* bed in the Gippsland Lakes (Poore 1982) had few dominant species in common with Swan Bay. These differences indicate that, as with communities associated with *P. australis* and *Z. capricorni*, there is no characteristic *Z. muelleri* or *H. tasmanica* community. Each site supports a faunal community that is determined by a range of environmental conditions of which the presence of seagrass is only one.

This study has produced quantitative data on the biomass of vascular hydrophytes of Port Phillip Bay. Like Westernport Bay, *H. tasmanica* is the dominant vascular hydrophyte present. The plant cover is shown to influence benthic macrofauna, the fauna of Swan Bay being apparently characteristic for the area and not particularly similar to other *Heterozostera-Zostera* communities in Victoria.

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THE GENUS *UPEROLEIA* GRAY (ANURA: LEPTODACTYLIDAE) IN QUEENSLAND, AUSTRALIA

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ABSTRACT: Four new taxa are described: *U. capitulata* sp. nov. from south-western Queensland and north-western N.S.W., *U. fusca* sp. nov. from northern coastal N.S.W. to the central Qld coast, *U. littlejohni* sp. nov. from north-central Qld and *U. mimula* sp. nov. from Cape York.

Uperoleia trachyderma Tyler, Davies and Martin and *U. inundata* Tyler, Davies and Martin are recorded from Queensland for the first time. The distribution of *U. lithomoda* Tyler, Davies and Martin is expanded and the morphology and osteology of the species are examined across its range. Previous descriptions of these taxa are supplemented with osteological data on the carpus, tarsus and ilium, and with descriptions of the hyoid.

A generic checklist and keys to species in Australia are provided.

The nomenclature of frogs of the genus *Uperoleia* Gray has been in a state of flux since the revision of Tyler, Davies and Martin (1981a) who showed the genus to comprise many more than the three named species [*Uperoleia marmorata* Gray, *U. rugosa* (Andersson) and *U. mjobergi* (Andersson)] recognised by earlier workers (Littlejohn 1967, Lynch 1971, Cogger 1975, Tyler 1976).

Tyler *et al.* (1981a,b,c) and subsequently Davies *et al.* (1985) were concerned mainly with species from the north and north-west of the continent, leaving the eastern Australian fauna largely unknown. Davies and Littlejohn (1986) amplified the redescriptions of *U. laevigata* Keferstein of Tyler *et al.* (1981a) and of *U. rugosa* of Tyler *et al.* (1981a) and Davies and McDonald (1985). They referred *U. fimbrianus* (Parker) to the synonymy of *U. rugosa* and described *U. tyleri* and *U. martini* from coastal N.S.W. and Victoria. A fourth species of *Uperoleia* has been reported from northern Queensland, namely *U. lithomoda* Tyler, Davies and Martin (Tyler & Davies 1984).

Our studies have revealed the occurrence of a further six species of *Uperoleia* in Queensland; four of these are undescribed. Here we describe the four new taxa, report range extensions of two species of *Uperoleia* into Queensland and supplement their descriptions, and provide additional data on the distribution and morphology of *U. lithomoda*.

MATERIALS AND METHODS

Material reported here is deposited in the American Museum of Natural History, New York (AMNH), Australian Museum, Sydney (AM), CSIRO Wildlife Collection, Canberra (ANWC), British Museum (Natural History), London (BMNH), Californian Academy of Sciences, San Francisco (CAS), Museum of Comparative Zoology, Harvard (MCZ), Museum of Natural History, University of Kansas, Lawrence (KU), Museum of Victoria, Melbourne (NMV), Northern Territory Museum, Darwin (NTM), Queensland Museum, Brisbane (QM), South Australian Museum, Adelaide

(SAM) and the University of Adelaide osteological collection (UAZ). Initials following these acronyms are departmental identifications within the institutions and generally precede the registration numbers on the tags attached to the specimens.

Most species of *Uperoleia* possess parotoid glands which cover the side of the head and obscure the tympana, and hence prevent accurate measurement of head length and head width. Measurements taken were: eye diameter (E), eye to naris distance (E-N), internarial span (IN), snout to vent length (S-V) and tibia length (TL). The methods of measurement follow Tyler (1968). Data are presented as mean \pm standard deviation with ranges in parentheses.

Osteological data were obtained from specimens cleared and stained with alizarin red S for bone after the method of Davis and Gore (1947), and with alizarin red S for bone and alcian blue for cartilage after the method of Dingerkus and Uhler (1977). Osteological descriptions follow Trueb (1979) and Andersen (1978) (for the carpus and tarsus).

Mating calls were recorded with a Uher 4000 Report Monitor tape recorder and an AKG D190 ES microphone, or a Sony TC510-2 tape recorder and a Beyer M88 dynamic microphone at a tape speed of 19 cm sec⁻¹. Wet bulb air temperatures were measured with a Schultheis rapid-reading thermometer close to the calling sites of males. Calls were analysed by means of a sound spectrograph (Kay Model 7800 digital Sona-Graph). Temporal characteristics of calls were determined from wide-band (300 Hz bandpass) and spectral characteristics from narrow band (45 Hz bandpass) spectrograms. Three calls of each male were analysed and mean values were calculated.

Line drawing outlines were made with the aid of a Wild M9 stereoscopic dissecting microscope with a 0.4 \times reducing lens, and a camera lucida. Vegetation descriptions follow Walker and Hopkins (1984).

Statistical analyses of morphological measurements follow Sokal and Rohlf (1981).

SYSTEMATIC ZOOLOGY

Uperoleia lithomoda Tyler, Davies and Martin

Uperoleia lithomoda Tyler, Davies & Martin 1981, Aust. J. Zool. Suppl. Ser. 79, p. 43.

Uperoleia variegata Tyler, Davies & Martin 1981a, p. 55.

Uperoleia lithomoda: Cogger 1983, p. 84; Cogger, Cameron & Cogger 1983, p. 33; Tyler & Davies 1984, p. 123 (part.); Tyler, Smith & Johnstone 1984, p. 99; Tyler 1985, p. 407; Tyler & Davies 1986, p. 59; Tyler, Davies & Watson 1986, p. 98; Tyler, Davies & Watson in press; Mahony & Robinson 1986, p. 120.

DEFINITION: A small species (males 19-26 mm S-V, females 17-30 mm S-V) of moderately-gross habitus and short limbs. Maxillary teeth absent; frontoparietal fontanelle poorly to moderately exposed; basal or no webbing between the toes; toes poorly to moderately fringed; eye to naris distance usually greater than internarial span; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent. Mating call an explosive tick of 4-6 pulses with a pulse repetition rate of 250-450 pulses sec⁻¹.

MATERIAL EXAMINED: W.A.: SAM R28741-3, swamp at spillway bridge, 11.5 km NE Lake Argyle Tourist Village (16°02', 128°47'); SAM R28744-56, WAM R94346-47, Gibb River Station in billabong behind Hstd; SAM R28757, WAM R94348-50, Gibb River Rd, 22.1 km NW Lennard River.

N.T.: AM R53619-20, 15 km N McArthur River Camp on Borrooloola Rd (16°15', 136°04'); R53352, 36.5 km N McArthur River Camp on Borrooloola Rd (16°16', 136°07'); R53693, 10 km N McArthur River Camp on Borrooloola Rd; R53732-5, approx. 15 km N McArthur River Camp on Borrooloola Rd (16°15', 136°04'); SAM R25110-11, 10.2 km from Katherine along Gorge Rd; R20447, 15 km from Katherine along Gorge Rd; R24010, 408 km W Katherine on Victoria Hwy; R24011-14, 11 km NE Katherine along Gorge Rd; R24015-16, Saddle Creek, Victoria Hwy; R25108-9, 17 km E Roper River Rd/Stuart Hwy Jen; R28758-61, 7 km W Mary River on Arnhem Hwy; R28762-64, Mary River Bridge, Arnhem Hwy; R25467-71, 2.7 km E Angurugu, Groote Eylandt; R27473, 8.2 km E Emerald River, Groote Eylandt.

Qld: NTM R11741, R11747, R11756-7, R11760, R11763, R11765 Westmoreland; SAM R28765-7, R29691-5, QM J45922, Kangaroo Rat Mine, Amber Station; SAM R28768, 1.6 km from Burlington Station on Amber Station Rd; SAM R28769, Amber Station near Lynd River Crossing (formerly QNPWS N28751); SAM R28770, James Cook University Experimental Farm "Fletcherview", Charters Towers; SAM R28771, Lakefield National Park Ranger Station (formerly QNPWS 28872); SAM R28773-5, QM J45997, J45988-91, UAZ A897 (formerly QNPWS 32319), Coen Airport (13°45'30", 143°06'30"); SAM R28772, Twin Humps, 12 km N Coen (13°51'30", 143°9'30"); QM J31554, Chillagoe; J19862, 1.6 km S Yorkeys Knob P.O.; J29859, 62 km from Townsville on Charters

TABLE 1
SNOUT-VENT LENGTH, TIBIA LENGTH/SNOUT-VENT LENGTH AND EYE-NARIS DISTANCE/INTERNARIAL SPAN MEASUREMENTS FOR SEVERAL POPULATIONS OF *Uperoleia lithomoda*. DATA ARE EXPRESSED AS MEAN ± STANDARD DEVIATION WITH RANGES IN PARENTHESES. DATA FOR MALES AND FEMALES ARE POOLED FOR RATIO CALCULATIONS.

		Gibb River Station W.A.	22.1 km NW Lennard River W.A.	Spillway Swamp W.A. (type locality)	Katherine N.T.	Mary River N.T.	McArthur River N.T.	Groote Eylandt N.T.	Edward River Qld	Amber Sin/Charters Towers Qld	All material examined
	n	14	6	4	15	7	8	10	26	12	102
S-V	♂	20.25 ± 1.08 (17.9-22.1)	22.83 ± 1.37 (21.5-25.1)	19.0 (17.8-20.5)	20.92 ± 1.66 (18.85-23.5)	18.76 ± 1.10 (16.7-20.1)	21.18 ± 1.24 (19.4-22.7)	24.6 ± 1.90 (20.0-26.5)	16.89 ± 0.76 (16-17.9)	21.9 ± 1.78 (18.3-24.5)	20.22 ± 2.67 (16-26.5)
	n	3	3	2	2			1	4		10
	♀	22.3 (20.3-23.6)	0.35 ± .02 (0.32-0.37)	0.36 (0.34-0.39)	(19.5-24.5)	0.35 ± .02 (0.34-0.40)	0.33 ± .02 (0.31-0.37)	29.5	18.58 (16.8-19.2)		21.76 ± 3.77 (16.8-29.5)
TL/S-V		0.35 ± .02 (0.31-0.39)	0.35 ± .02 (0.32-0.37)	0.36 (0.34-0.39)	0.34 ± .02 (0.31-0.37)	0.35 ± .02 (0.34-0.40)	0.33 ± .02 (0.31-0.37)	0.36 ± .03 (0.32-0.44)	0.36 ± .02 (0.31-0.41)	0.37 ± .02 (0.33-0.42)	0.35 ± .02 (0.31-0.42)
E-N/IN		1.27 ± .18 (1.00-1.64)	1.33 ± .17 (1.13-1.57)	1.13 (1.00-1.31)	1.35 ± .25 (0.94-1.75)	1.44 ± .28 (1.13-1.89)	1.35 ± .23 (1.13-1.85)	1.25 ± .17 (1.00-1.53)	1.23 ± .19 (0.83-1.60)	1.20 ± .20 (0.95-1.53)	1.28 ± .22 (0.83-1.89)

Towers Rd; J29884, 96 km from Townsville on Charters Towers Rd; SAM R24349 (24), 1 km E Edward River Township; R24343-8, Edward River Township; SAM R28776, R29696, QM J45993, Pajingo Station (146°11', 20°47'); SAM R28777-9, R29697, QM J45994, Battery Station, Snake Creek (145°39', 19°27'); SAM R28780, QM J45995, Occupation licence 117 (145°13', 20°40'); QM J45996, Lockwall Station (145°51', 19°54'); QM J42533, J42536, 20 km W Cooktown; QM J38842-56, Pentland, N side of town; J38874-75, 18 km W Torrens Creek; AM R38449-54, Rocky Creek, 40 km S Batavia Downs, Cape York.

EXTERNAL MORPHOLOGY: The specimens were arbitrarily divided into eight populations on a geographic basis: Gibb River, W.A., Lennard River environs, W.A., Katherine area, N.T., Mary River (Arnhem Hwy) area, N.T., Groote Eylandt, N.T., McArthur River area, N.T., Edward River township, Qld, and Amber Station area, Qld. Measurements from these populations are shown in Table 1.

An F_{\max} test for homogeneity of variances is not significant and a one way analysis of variance of size is highly significant ($F=46.25$) indicating size differences between different populations. A GT_2 method of multiple comparison amongst pairs of means based on unequal sample sizes gave results depicted in Table 2. There is no geographic cline in these data.

The shape of the snout can vary from moderately truncate to quite sharply pointed even within one population (Fig. 1). The sharply-pointed snouts (Fig. 1C) are not common and within any population about equal proportions of blunt and gently-rounded snouts occur. The exception is in the Gibb River Station population where more blunt-snouted specimens were observed. Within this sample are the paratypes of *U. variegata* Tyler Davies and Martin referred to the synonymy of *U. lithomoda* by Tyler *et al.* (in press).

These specimens were collected in the dry season from underground and appear to have been preserved in strong fixative. They are somewhat dehydrated and distortion of snout shape has occurred (see Davies & Littlejohn 1986). The higher proportion of blunt-snouted individuals in this population thus may be an artifact. The nostrils are usually located dorsolaterally but are occasionally almost dorsal.

Rugosity of the dorsum is usually moderate (Fig. 2) except in material collected in the dry season (e.g. Gibb River and McArthur River) when equal proportions of moderately- and poorly-rugose dorsa are recorded. Parotoid glands are always well developed (Fig. 2). Inguinal glands also are well developed except in most of the *U. variegata* paratypes collected in the dry season, presumably when glandular activity is minimal (see McDiarmid 1968). Coccygeal glands are usually well, or occasionally moderately developed, except, again, in the dry season Gibb River material in which these glands are poorly developed.

The pattern of the dorsum of *U. lithomoda* is usually strongly defined. Ground colour is usually grey with brown or black markings often highlighted with rust-coloured spots. Dark crescentic markings are usually medial to the parotoid glands in the scapular area and are often raised in the form of lyrate plicae (Fig. 3). Scapular plicae are present except in the Edward River and Gibb River populations in which they are absent in a third of individuals. Gold colouring on the dermal glands produces yellow-gold lateral stripes in most specimens (Fig. 2).

Subarticular and palmar tubercles on the hand are usually prominent, or moderately prominent. The presence of supernumerary tubercles on the hand varies. The palmar tubercle at the base of the thumb is generally small and masked by the unpigmented nuptial pad in most males.

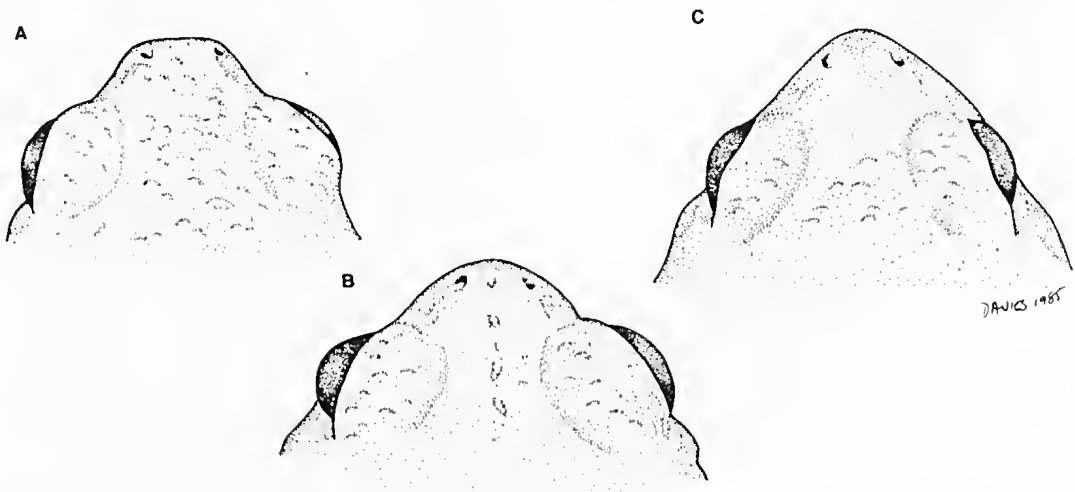


Fig. 1 — Dorsal views of the heads of *Uperoleia lithomoda* from Gibb River Station, W.A. A, blunt. B, rounded C, sharp.



Fig. 2—*Uperoleia lithomoda* in life (Katherine, N.T.).

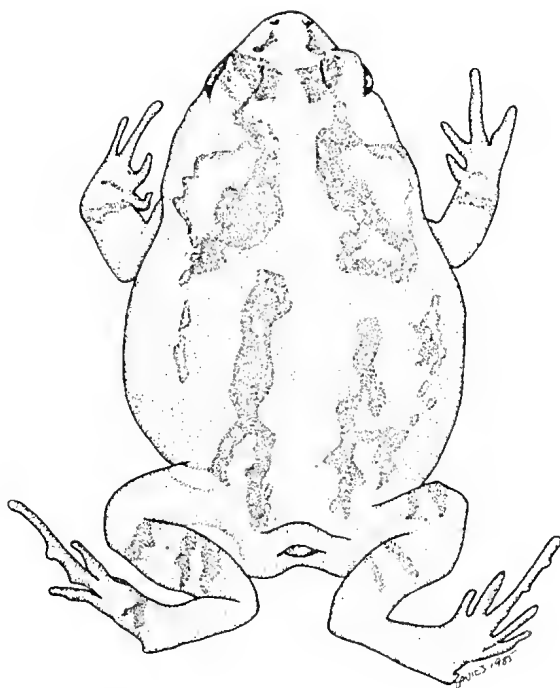


Fig. 3—Dorsal pattern in *Uperoleia lithomoda* (SAM R25468).

Fringing on the toes ranges from poor to moderate. Preservation influences this feature; freshly- and carefully-preserved material tends to have more pronounced fringing than less well-preserved material. In most populations moderately fringed toes are typical except for the Mary River and Edward River populations. Toe webbing is either absent, or basal, usually in about equal proportions. In the Edward River populations, however, 27 of 30 specimens lacked toe webbing. Variation in toe webbing and fringing is shown in Fig. 4. Both inner and outer metatarsal tubercles are particularly prominent in *U. lithomoda* (Figs. 2, 4). The outer metatarsal tubercle is usually aligned in a plane perpendicular to the long axis of the foot, occasionally slightly angled. Subarticular tubercles are conical and not very prominent.

The ventral skin is usually highly granular except in material collected in the dry season at Gibb River, and in some of the material collected at this site at the beginning of the wet season. Granularity is less prominent in the few females examined, than in males. White flecks often are present in the centre of the granules. Ventral pigmentation is rare other than on the throat in calling males. If present, it is in the form of a faint dusting of individual pigment granules usually visible only with a microscope. Groote Eylandt and Edward River material shows greater ventral pigmentation than other specimens. Inguinal patches are not always apparent. When present, they are not as prominent as femoral patches. A faint or moderately-developed midvertebral stripe is almost always present.

TABLE 2

MULTIPLE COMPARISONS AMONGST PAIRS OF MEANS OF SNOUT-VENT LENGTH OF *Uperoleia lithomoda* AT EIGHT LOCALITIES, BASED ON UNEQUAL SAMPLE SIZES—GT; METHOD. THE DIFFERENCES SIGNIFICANT AT THE 5% LEVEL ARE INDICATED BY AN ASTERISK. Localities are as follows: 1 Edward River, Qld; 2 Mary River, N.T.; 3 Gibb River, W.A.; 4 Katherine and environs, N.T.; 5 McArthur River environs, N.T.; 6 Amber Station environs, Qld; 7 Lennard River environs, W.A.; 8 Groote Eylandt, N.T.

Ranked localities	1	2	3	4	5	6	7	8
1	—	2.277	1.7727	1.7337	2.1621	1.8664	2.4217	1.8664
2	1.87	—	2.4753	2.4479	2.7674	2.5433	2.9749	2.6352
3	3.36*	1.49	—	1.3807	2.370	2.1037	2.6093	2.214
4	4.03*	2.16	0.67	—	2.3414	2.0715	2.5818	2.1832
5	4.29	2.42	0.93	0.26	—	1.5441	2.8879	2.5365
6	5.01*	3.14*	1.65	0.98	0.72	—	2.674	2.2897
7	5.94*	4.07	2.58	1.91	1.65	0.93	—	2.7613
8	7.71*	5.84*	4.35*	3.68*	3.42*	2.70*	1.77	—

OSTEOLOGY: *Material examined*: W.A.: SAM R17220, Granite Creek, 14.1 km NE Lake Argyle Tourist Village (Paratype); UAZ A769, A808, Spillway Bridge Swamp 11.5 km N Lake Argyle Tourist Village (Topotypes); SAM R17219, Gibb River Hstd garden; UAZ A767-8, A781-98, Swamp behind Gibb River Station Hstd billabong; UAZ A780, B896, 22.1 km NW Lennard River on Gibb River Rd.

N.T.: SAM R17218, Arnhem Hwy at Fogg Dam turnoff, 24 km ESE Darwin; UAZ A809, Mary River

Bridge on Arnhem Hwy; UAZ A807, 6.4 km N Katherine along Gorge Rd; UAZ A799-806, A811, B812, 2.7 km E Angurugu, Groote Eylandt, ANWC A1085, Elcho Island.

Qld: UAZ A897 (formerly QNPWS N32319), Coen Airport; UAZ A810, Edward River township; SAM R29691-2, Kangaroo Rat Mine, Amber Station; SAM R28771, Lakefield Ranger Station; AMR 38450, Rocky Creek, 32 km S Batavia Downs; QM J31554, Chillagoe; J19862, 1.6 km S Yorkeys Knob P.O.; J29859, 62 km

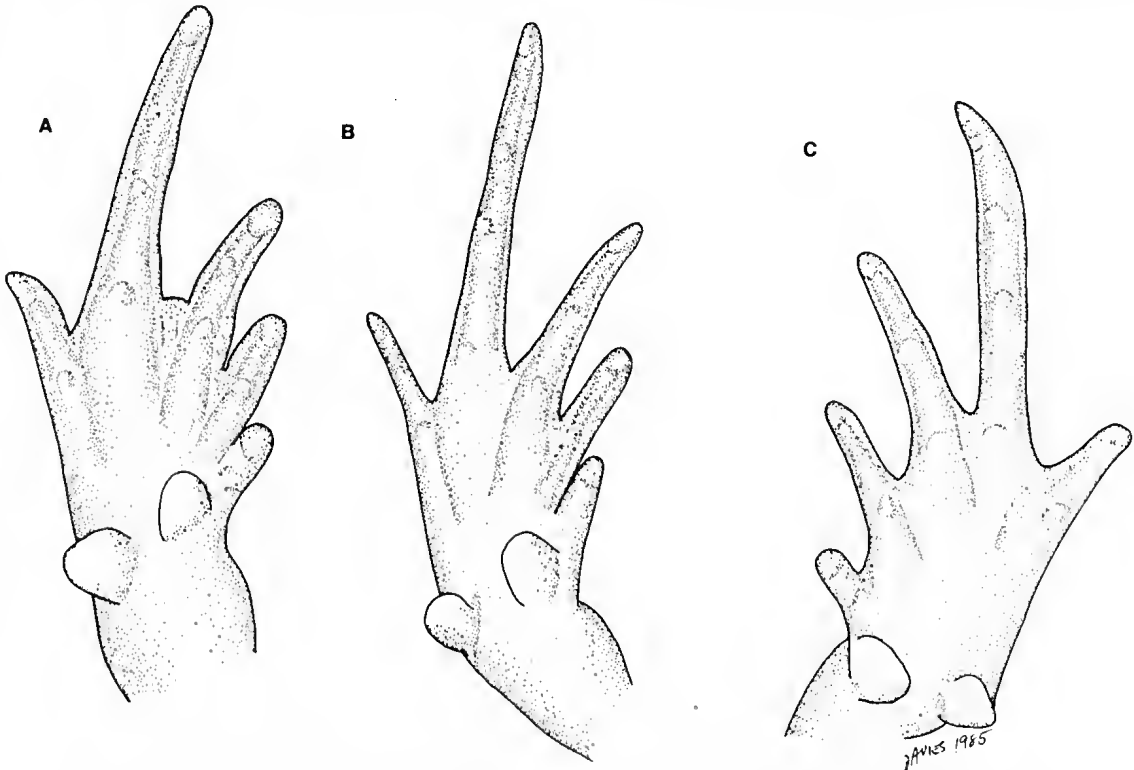


Fig. 4—Variation in the toe webbing and toe fringing in *Uperoleia lithomoda*. A, basal webbing, well fringed, Amber Station, Qld. B, unwebbed, moderate fringing, Gibb River Station, W.A. C, unwebbed, unfringed, Mary River, N.T.

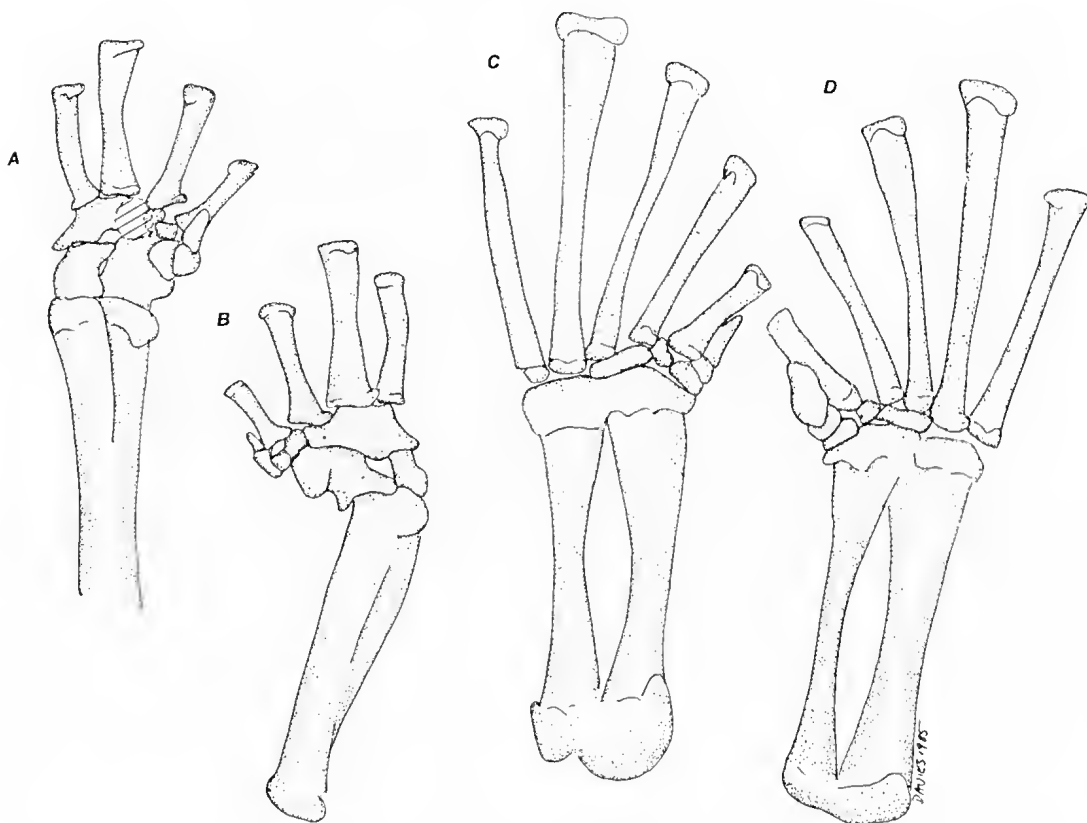


Fig. 5—*Uperoleia lithomoda*, Gibb River, W.A. A, Ventral and B, Dorsal views of carpus. C, Dorsal and D, Ventral views of tarsus.

from Townsville on Charters Towers Rd; J29884, 96 km from Townsville on Charters Towers Rd; J29483, 1 km S Laura; J29316, 1 km E Laura on Laura-Cooktown Rd; SAM R29696, Pajingo Station; R29697, Battery Station; J38545, J38856, J38842, J38844, Pentland, N side of town.

The osteological description of *U. lithomoda* by Tyler *et al.* (1981a) did not include elements of the carpus, tarsus, pelvic girdle or hyoid. These features have proved useful as species characters (Davies & Littlejohn 1986), and we here supplement the original description.

Carpus: The carpus consists of six elements. Quite considerable torsion occurs. Both the O. ulnare and O. radiale are present. The O. radiale is the larger. These elements articulate with the O. radioulna proximally, and with each other on their proximo-medial border. Distally both elements articulate with the large transversely-elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale. The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. From the lateroproximal corner a small, subacuminate flange extends proximally. Ventromedially a palmar sesamoid occurs (Fig. 5). The O. centrale preaxiale articulates laterally with the O. radiale and distally with the O. centrale postaxiale, and with the carpal element of the O. distale carpal 2 (Fig.

5), and laterally with the basal prepollical element. The carpal element of the O. distale carpal 2 articulates with, but is not fused to, the carpal element of the O. distale carpal 3.

Tarsus: The O. tibiale and O. fibulare are elongated elements fused proximally and distally. The O. tibiale extends as far as the distal end of the O. fibulare. Three distal tarsal elements are present. The lateral element is the largest and lies at the base of O. metatarsus III (Fig. 5). It extends laterally to articulate with the medioproximal side of the base of O. metatarsus II. The second element lies at the base and slightly laterally to O. metatarsus II. The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal element of the prehallux is large and extends approximately one half the length of O. metatarsus I (Fig. 5).

Ilium: No ilial crest is developed. The dorsal prominence is wedge-shaped and extremely prominent (Fig. 6). The dorsal protuberance is prominent and posterolateral.

Hyoid: The hyoid plate is approximately as wide as it is long. The alary processes are prominent but not pedunculate. The anteromedial processes of the anterior hyale are short and slender. The posterolateral processes of the hyoid plate are moderately broad and moderately long. The posterior cornua are ossified (Fig. 6).

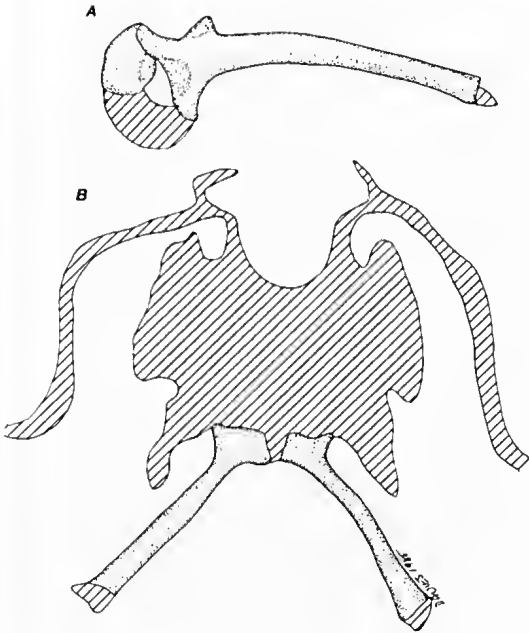


Fig. 6—*Uperoleia lithomoda* (UAZ B896). A, Lateral view of ilium and B, Ventral view of hyoid.

VARIATION: Skulls of *U. lithomoda* share a combination of features: nasals that are closely-applied anteromedially and widely-separated posteromedially with a crescentic anteromedial edge, and frontoparietals that curve anteromedially on their orbital edges (Fig. 7). Exposure of the frontoparietal fontanelle varies from almost completely roofed with posteromedial fusion of the frontoparietal elements (Fig. 7C) to moderately-widely exposed in young specimens (Fig. 7A). The more common condition is a poorly-exposed frontoparietal fontanelle as shown in Fig. 7B. Approximately one half of the specimens examined had state B, one third had a condition between states B and C and the remainder, state C.

The otic ramus of the squamosal has two conditions; it is short (Fig. 7B) or moderately long (Fig. 7C). The zygomatic ramus of the squamosal is short in all specimens and does not vary. The prootic and exoccipital are never fused (although calcification is common) and ossi-

fication of the exoccipitals dorsomedially and ventromedially is always absent. The carotid canal groove is rarely apparent (4 specimens in 48). The palatal shelf is invariably deep. The palatine processes of the premaxillaries are either short and broad or moderately long and slightly more slender. Separation of these elements varies; those exhibiting the short and broad condition tend to be more closely applied than the others. The pterygoid process of the palatal shelf is moderately well developed in all cases.

The palatines are slender and slightly overlap the anterior extremities of the sphenethmoid in ventral view. They are reduced laterally, and do not extend beyond the lateral extremities of the maxillary processes of the nasals. They are slightly expanded medially in many cases and usually angled fairly acutely to the sphenethmoid at an angle approaching 45° ; more rarely the angle is slightly flatter.

The cultriform process of the parasphenoid is only moderately broad either reaching the level of the medial extremities of the palatines or not so far. The anterior extremities are slightly serrate, but truncate. The alae of the parasphenoid are at right angles in all but one specimen from Groote Eylandt (the exception is angled slightly posterolaterally). The alae are moderately short, not reaching the extremities of the medial rami of the pterygoids.

The pterygoids are robust. The anterior rami are moderately slender and in moderately long contact with the pterygoid process of the palatal shelf of the maxillaries. The posterior ramus is short, moderately broad and moderately acute. The medial ramus is moderately long (occasionally longer), acuminate, and not in bony contact with the prootic region.

The pars facialis of the maxillary is shallow with a very well-developed preorbital process. The alary processes of the premaxillaries are perpendicular to the pars dentalis, moderately broad at the base and usually bifid dorsally.

Vomerine remnants are absent in all the material examined and invariably a bony columella is present.

HABITAT: *U. lithomoda* calls at the base of grass tussocks usually on coarse gravelly soil at some distance from ephemeral water (Tyler, Watson & Davies unpubl.). If two or more species are calling at the same

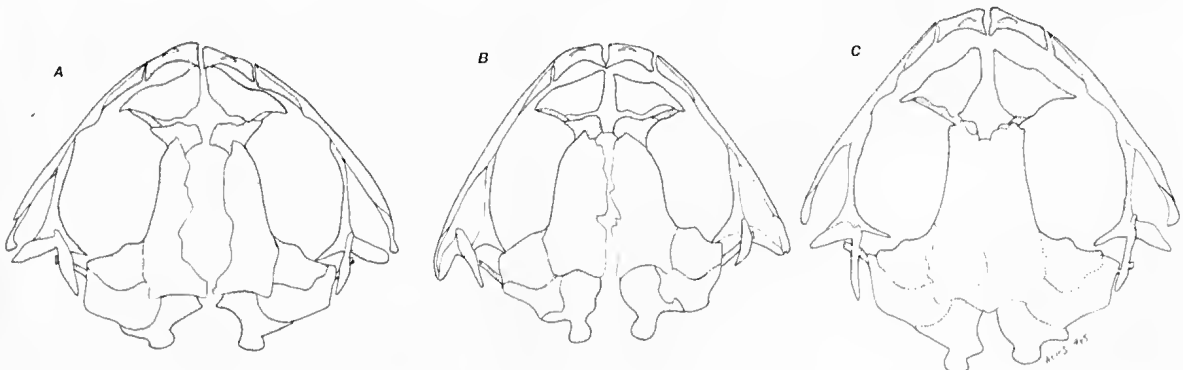


Fig. 7—Dorsal views of skulls of *Uperoleia lithomoda*. A, C, from Gibb River, W.A. B, from Coen, Qld.

site, the other species (e.g. *U. inudata* on Groote Eylandt and *U. borealis* at Granite Creek in W.A.) calls closer to the water than *U. lithomoda*. Spatial separation is extreme in these situations (Tyler *et al.* 1986). However, at Lakefield (Cape York), *U. lithomoda* and *U. mimula* called at the base of tussocks on inundated floodplain and no spatial separation was apparent. Habitat here included *Melaleuca* woodland, eucalypt woodland, open woodland and eucalypt forest with tussock or sod grassland understorey.

ADVERTISEMENT CALL: Advertisement calls of *U. lithomoda* were described and analysed by Tyler *et al.* (1981a,c). The call is an explosive click that is painful to the ears, in a large chorus. We have examined calls from across the range of *U. lithomoda* in Queensland and find little variability (Table 3). Tyler *et al.* (in press) found the population at Gibb River Station to have fewer pulses per note than those from Lake Argyle and Katherine (which are similar to the Queensland calls analysed here). The result is a considerable lowering of pulse repetition rate (62.5-234.7 pulses sec⁻¹ compared with 150-462). This was interpreted as a continuation of an east west trend (substantiated by the data here). Because of the overall similarity of calls of this popula-

tion with others, the conspecificity of the material was accepted.

DEVELOPMENTAL BIOLOGY: Tadpoles are dark brown on the dorsal and lateral surfaces. The body is flattened dorsally (Fig. 8) with dorsally-located nostrils. The spiracle is sinistral and the vent dextral. The fin is pigmented with islands of fine pigment, the tail tip being black (Fig. 8). The myotomes are mottled with pigment.

The mouth disc is very small. The tooth formula is $\frac{2}{3}$ with the lower of the upper rows divided (Fig. 8). The horny beak is weakly developed. A very poorly-developed border of papillae, widely separated anteriorly and posteriorly, surrounds the oral disc.

DISTRIBUTION: *Uperoleia lithomoda* occurs in the Kimberley Division of Western Australia, in the north of the Northern Territory, on Groote Eylandt, at the base of the Gulf of Carpentaria, and on the Cape York Peninsula. Tyler and Davies (1984) reported the species to occur in New Guinea, but this record is not sustained in view of the information now available on the second species known to occur on Cape York. This cryptic species is described on p. 178 and is morphologically very similar to *U. lithomoda*. The distribution of *U. lithomoda* is shown in Fig. 9.

TABLE 3
ADVERTISEMENT CALL CHARACTERISTICS OF THREE SPECIES OF *Uperoleia*.

Species & Locality	N	No. of pulses msec	Duration	Pulse repetition rate (pulses sec ⁻¹)	Dominant Frequency Hz	Wet bulb temperature °C
<i>Uperoleia lithomoda</i> J.C.U. experimental farm nr Charters Towers (SAM R28870, formerly NPWS N15592)	1	3	13 (10-15)	260 (200-300)	2367 (2300-2400)	24.6°
<i>U. lithomoda</i> Amber Station (SAM R28769, formerly NPWS N28751)	1	3.67 (3-4)	19.3 (18-20)	174 (150-222)	2500	—
<i>U. lithomoda</i> Lakefield (SAM R28771, formerly NPWS N28872)	1	3	11.8 (10-15)	250 (200-300)	3320 (3300-3400)	25.2°
<i>U. lithomoda</i> Coen Airport (UAZ A897, formerly NPWS N32319)	1	3.2 (3-4)	12.2 (10-16)	265 (231-300)	2520 (2500-2600)	24.8°
<i>U. lithomoda</i> 9.6 km N Coen (SAM R29772, formerly NPWS N32388)	1	5.5 (5-6)	21 (20-22)	261 (250-272)	2750 (2700-2800)	24.6°
<i>Uperoleia fusca</i> Type locality (SAM R29596, R29599-29602)	5	20.6 (18-24)	302.1 (220-360)	68.41 (64.86-73.08)	2700	21.5°-23.1°
<i>Uperoleia mimula</i> Townsville Town Common (SAM R29631, R29634-5)	3	4.1 (3-5)	65.5 (55-90)	64.1 (56-83)	2900 (2600-3300)	23.4°-24.0°
<i>U. mimula</i> Lannercost, S.F. (SAM R29627, formerly NPWS N15605)	1	4.7 (4-5)	64 (50-70)	73.5 (71-80)	2750 (2700-2800)	24.8°
<i>U. mimula</i> Bazant Outstation (QM J45943)	1	4.3 (4-5)	43 (40-50)	100 (100)	2800 2800	27.2°

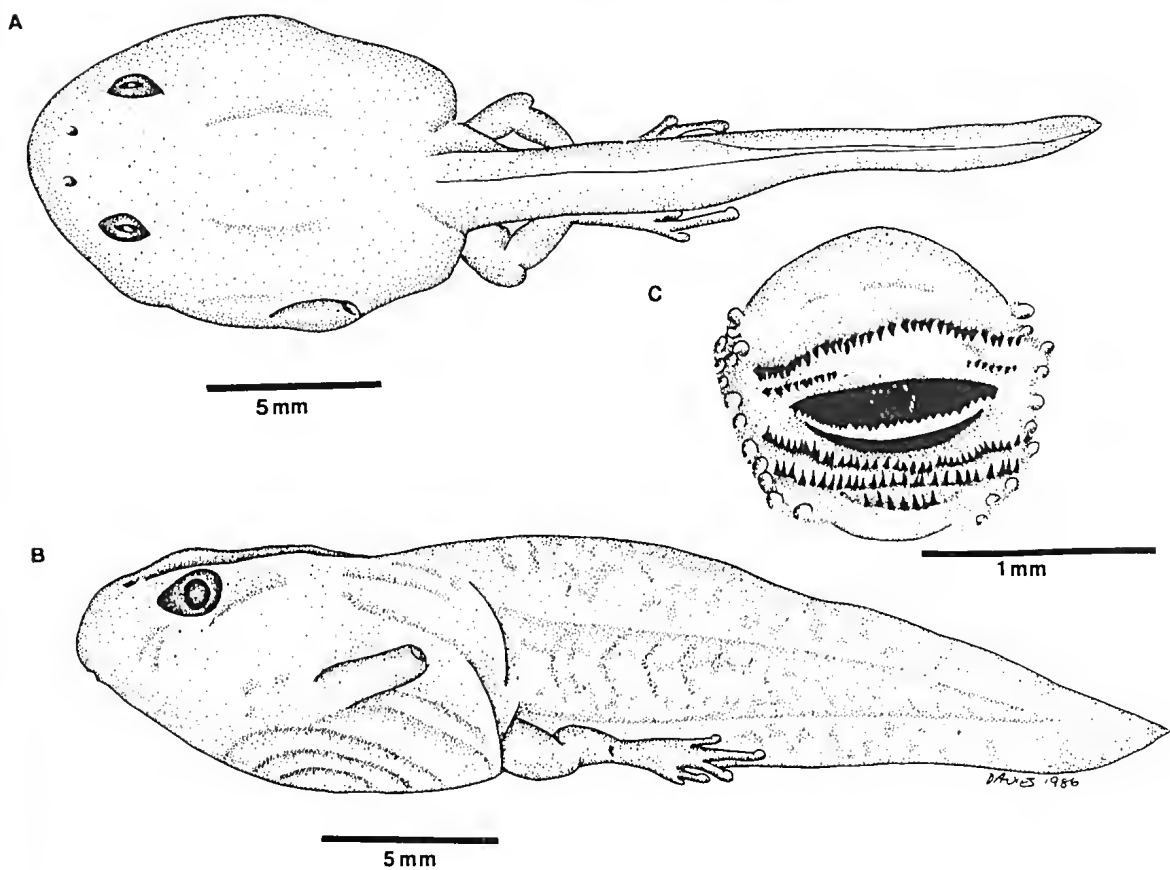


Fig. 8—*Uperoleia lithomoda* tadpole, stage 40 of Gosner (1960), from Newry Station, N.T. A, Dorsal and B, lateral views. C, oral disc.

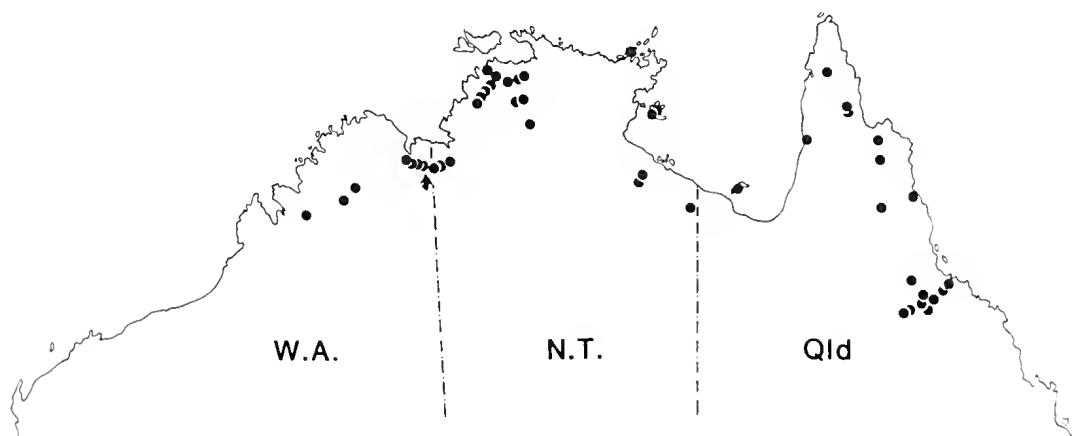


Fig. 9—Distribution of *Uperoleia lithomoda*. The arrow indicates the type locality.

COMPARISON WITH OTHER SPECIES: *Uperoleia lithomoda* is a small to moderately large species (males 19–26 mm, females 17–30 mm) lacking maxillary teeth and with a poorly- to moderately-exposed frontoparietal fontanelle. These features are shared by *U. aspera*, *U. rugosa*, *U. mimula* and *U. capitulata*.

From *U. aspera*, *U. rugosa* and *U. capitulata*, *U. lithomoda* can be distinguished by a combination of lyrate scapula plicae, gold-tipped parotoid and inguinal glands giving the impression of yellow to cream lateral stripes on the dorsum, and by a very short call consisting of 4–6 rapid pulses.

U. lithomoda is most closely related to *U. mimula*. From this species *U. lithomoda* can be distinguished by the presence of prominent markings on the dorsum, by the lack of ventral pigmentation, by strong development of lateral golden, yellow gold or cream stripes on the dorsum (sometimes developed in *U. mimula*) and by call. (The pulses of the calls of *U. lithomoda* are difficult to delineate whereas those of *U. mimula* are recognisable to the ear—see Fig. 33).

Uperoleia inundata Tyler, Davies and Martin

Pseudophryne fimbriatus? : Parker 1926, p. 670 (part.)
Glauertia orientalis: Parker 1940, p. 67 (part.) Mitchell 1955, p. 404.

Uperoleia orientalis: Tyler, Davies & Martin 1981a, p. 24 (part.)

Uperoleia inundata: Tyler, Davies & Martin 1981, Aust. J. Zool. Suppl. Ser. 79, p. 39.

Uperoleia sp.: Gow, 1981, p. 66.

Uperoleia inundata: Daugherty & Maxson 1982, p. 342; Tyler, Crook & Davies 1983, p. 435; Cogger 1983, p. 83; Cogger, Cameron & Cogger 1983, p. 32; Tyler & Miller 1985, p. 45; Tyler 1985, p. 407; Maxson & Roberts 1985, p. 293; Tyler & Davies 1986, p. 58; Tyler, Davies & Watson 1986, p. 97; Mahony & Robinson, 1986, p. 120.

DEFINITION: A small to moderate-sized species (males 18–29 mm S-V, females 22–32 mm S-V) lacking maxillary teeth; toe webbing basal or absent; parotoid glands prominent; inguinal glands prominent and restricted to inguinal region; frontoparietal fontanelle widely exposed; carpus of six elements; anteromedial processes of anterior hyale of hyoid small and slender; ilial crest absent; dorsum generally smooth; call a short rasp with a pulse repetition rate of 68–163 pulses sec⁻¹.

MATERIAL EXAMINED: N.T.: SAM R28645–82, UAZ A829–36, B851–7, 1 km NE Jabiru East Watertank; SAM R28683–28712, UAZ A837–44, B858–61, swamp, 0.4 km from Jabiru East turnoff, Arnhem Hwy; SAM R28713, road to Radon Springs, foot Mt Broekman; SAM R28740, UAZ A596, Chickenhawk Dreaming, 2 km S Cannon Hill; SAM R28716–29, road from Retention Ponds 1 and 2, Jabiru; SAM R28730–33, UAZ A845–8, Retention Pond no. 4, Jabiru; SAM R28734–39, 8 km W Mary River on Arnhem Hwy; SAM R28714–5, 1 km NE Jabiru East turnoff Arnhem Hwy; NTM R12066, Scrutons Lagoon; AMNH I17726, CAS 156682–3, BMNH 1984.9–10, MCZ A106702, NTM R12527, R12532–44, SAM R25539–44, 8.2 km N Emerald River, Groote

Eylandt; AM R112420, NTM R12529, 18.3 km E Angurugu Airport, Groote Eylandt; AM R11249, KU 196728, NTM R12530, 5.6 km E Angurugu Airport, Groote Eylandt; KU 196729, NTM R12531, SAM R25545, Amagula Pools, Groote Eylandt; AM R53299–303, Caranbirini W.H., approx. 21 km from McArthur River (16°18', 136°05'); AM R53351, R53353, 36.5 km N McArthur River Camp on Borrooloola Rd (16°06', 136°07'); AM R53506, R53616–18, R53621, R53736–8, 15 km N McArthur River Camp on Borrooloola Rd (16°15', 136°04'); AM R53691–2, 10 km N McArthur River Camp on Borrooloola Rd; SAM R12741–74, R14186, Fish River Gorge; SAM R12743, R13864, 15.4 km S Hayes Creek.

Qld: NTM R12070, Westmoreland.

EXTERNAL MORPHOLOGY: Specimens of *U. inundata* from mainland Australia are smaller than those on Groote Eylandt (Tyler *et al.* 1986). The largest males examined from the mainland are 26 mm S-V and females 27 mm S-V compared with 29 mm S-V for males and 32 mm S-V for females on Groote Eylandt. Apart from size, the species is morphologically conservative. The snout is relatively narrow [E-N/IN 1.41 ± .21, (0.93–2.00)] and in Groote Eylandt specimens and some mainland specimens it protrudes beyond the lower jaw (Fig. 10). Approximately equal numbers of specimens have rounded or truncate snouts when viewed from above.

The hind limbs are short [TL/S-V 0.34 ± .02, (0.30–0.37)] and on Groote Eylandt specimens are even shorter (0.32 ± .02, Tyler *et al.* 1986).

The fingers are very rarely fringed. Subarticular tubercles are moderately prominent (Fig. 11). Palmar tubercles are very poorly developed, particularly that at the base of the thumb. This is scarcely detectable in males as it is masked by the unpigmented glandular nuptial pad.

Fringing on the toes is poor in most of the specimens examined but moderately to well-fringed in the rest. Toe fringing is absent in Jabiru material but present in southern Gulf of Carpentaria material. Toe webbing is absent in about one quarter of the specimens examined and basal in the remainder. About one-third of this basally-webbed material exhibits a slightly tubercular nature in this basal webbing (Fig. 11). Subarticular tubercles are conical. The inner metatarsal tubercle is oriented along the axis of the first toe and the outer metatarsal tubercle is angled to the long axis of the foot. The metatarsal tubercles are particularly large in Groote Eylandt and southern Gulf of Carpentaria material, but smaller and slightly compressed in much of the Jabiru material, giving the appearance of possible abrasion and wear.

The dorsum is smooth in most of the specimens examined and mildly tubercular in the remainder. The parotoid glands are prominent in all specimens and usually are cream. Inguinal glands are always prominent and always truly inguinal, being discreet and never extending anteriorly along the flanks. Coccyeal glands are usually very pro-

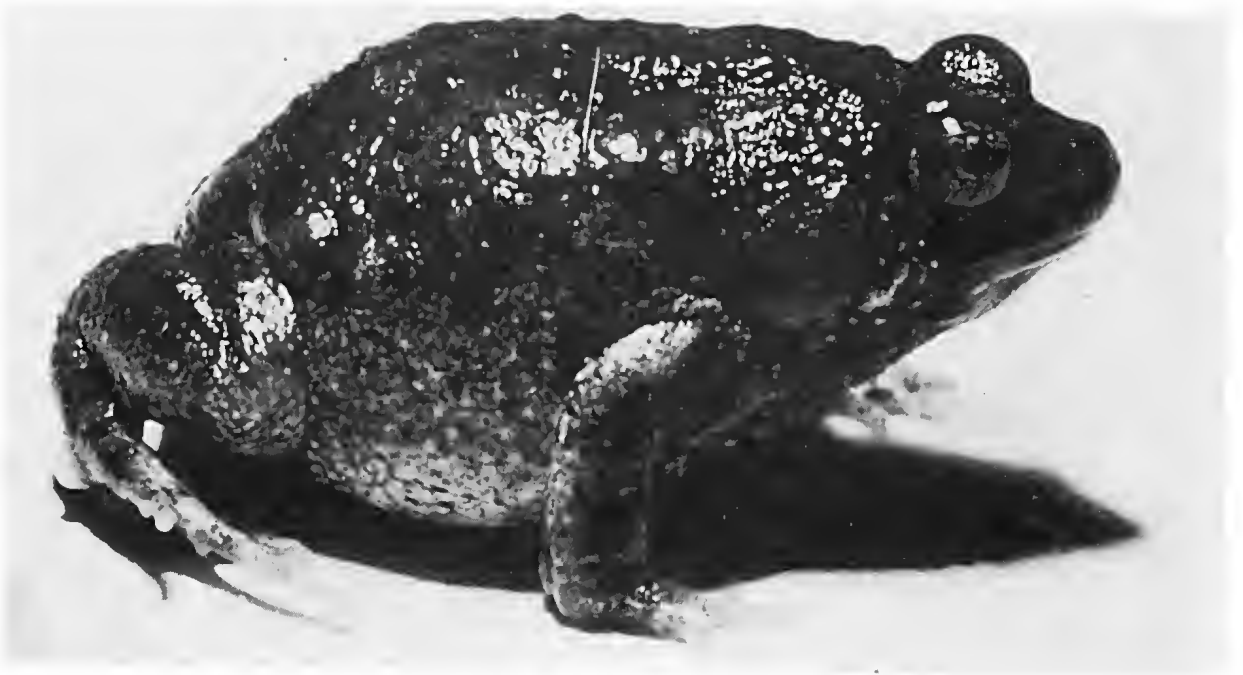


Fig. 10—*Uperoleia inundata* in life (Groote Eylandt).

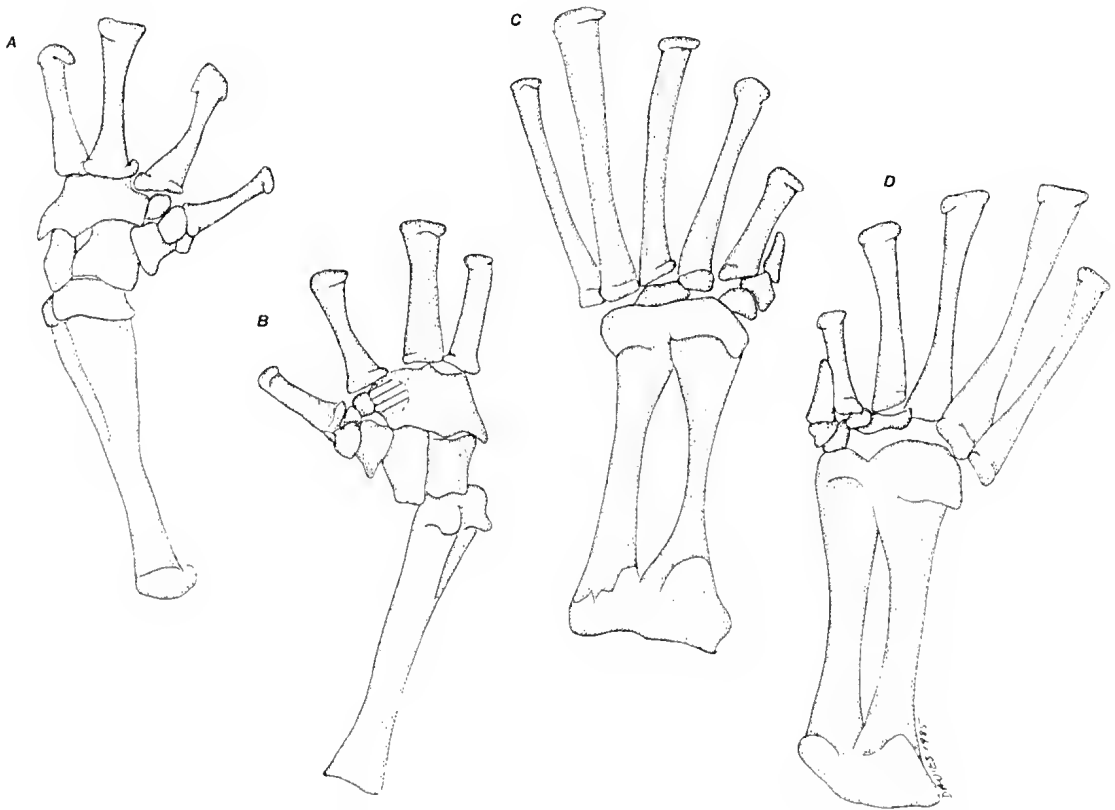


Fig. 12—*Uperoleia inundata* (UAZ A397). A, Dorsal and B, Ventral views of carpus. C, Dorsal and D, Ventral views of tarsus.

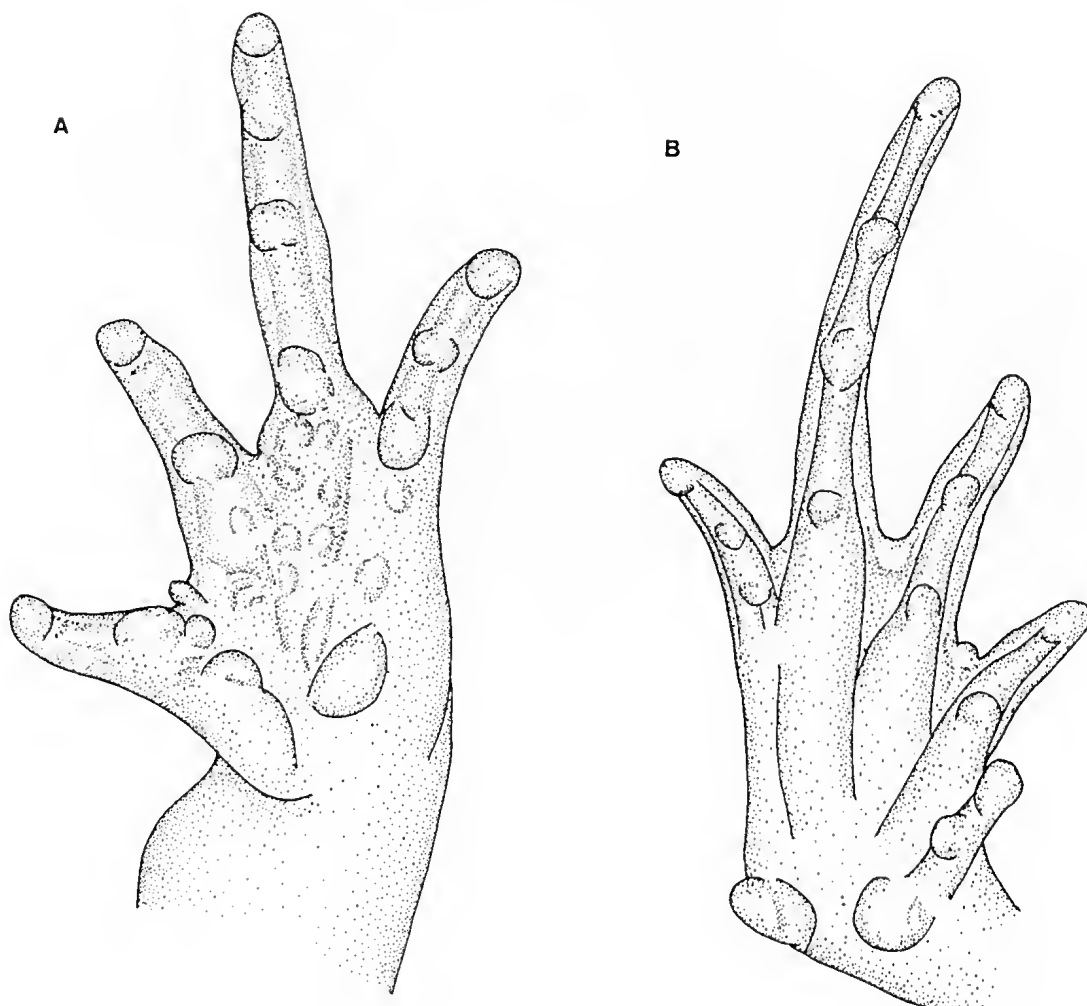


Fig. 11 — *Uperoleia inundata* (Groote Eylandt) (NTM R12529). A, Palmar view of hand. B, Plantar view of foot.

minent. The submandibular gland is discreet or disrupted in approximately equal proportions.

Scapular plicae are absent. Anterior eyeflaps are very poorly developed and cloacal flaps are poorly fimbriated. The ventral surface is granular in most of the specimens but is occasionally smooth. Dorsal patterning is very indistinct in most material; when present it is in the form of blotches of pigment with no strong outline.

Ventral pigmentation is absent in about two thirds of the specimens and faint in the remainder. Groote Eylandt material is slightly more ventrally pigmented than mainland material.

Inguinal and femoral patches are not prominent.

OSTEOLOGY: Material examined: N.T.: UAZ A818-826, 100 m E Jim Jim Turnoff, Arnhem Hwy; UAZ A827, Jabiru East Airstrip; UAZ A829-36, B851-57, Western end Jabiru East Airstrip; UAZ A837-44, B858-61, swamp, 0.4 km S Jabiru East turnoff; UAZ A845-48, Retention Pond no. 4; AUZ A849-50, Daly River Rd; UAZ A596, Chickenhawk Dreaming, 2 km S Cannon Hill;

UAZ A395(2), SAM R17268, Fish River Gorge; UAZ B397, B479, Darwin; UAZ A898, SAM R25540-41, Groote Eylandt.

The osteological description of *U. inundata* of Tyler *et al.* (1981a) did not include elements of the carpus, tarsus, pelvic girdle and hyoid. Here we supplement the original description.

Carpus: The carpus consists of six elements. Quite considerable torsion occurs. Both the O. ulnare and O. radiale are present; the O. radiale is the larger. These elements articulate with the O. radioulna proximally and with each other on their proximo-medial borders. Distally, both elements articulate with the large, transversely-elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale. The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. From the lateroproximal corner, a small flange extends proximally. Anteroventrally a palmar sesamoid is located. The O. centrale preaxiale articulates laterally with the O. radiale, distally with the O. centrale postaxiale and

with the carpal elements of the O. distale carpal 2 and 3 and laterally with the basal prepollical element (Fig. 12).

Tarsus: The O. tibiale and O. fibulare are elongated elements fused together at either end. The O. tibiale extends as far as the distal end of the O. fibulare. Three distal tarsal elements are present. The lateral element is the largest, and lies at the base of O. metatarsus III. It extends laterally to articulate with the medioproximal side of the base of O. metatarsus IV and medially to the base of O. metatarsus II. The second element lies at the base of O. metatarsus II. The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal prehallucal element is moderately broad and elongate, extending for approximately half the length of O. metatarsus I (Fig. 12).

Pelvic Girdle: No ilial crest is present. The dorsal prominence is small, gently monticuline, with a dorsolateral protuberance (Fig. 13). The pubis is calcified.

Hyoid: The hyoid plate is longer than wide. The antero-medial processes of the anterior hyale are small and slender. The alary processes of the hyoid plate are not pedunculate. The posterolateral processes are slender and moderately long. The posterior cornua are ossified (Fig. 13).

VARIATION: The nasals are only moderately ossified, widely-separated posteromedially and with characteristic indentations and erenulations on the posterior edge (Fig. 14). Lack of ossification giving indentations on posterior edges is common in *U. inundata*. The nasals are very occasionally crescentic on their anteromedial edges.

The frontoparietal elements characteristically extend anterolaterally to the poorly-ossified sphenethmoid. In most specimens the orbital edges are very straight and perpendicular to the prootic. In a few specimens they are inclined slightly medially (Fig. 14). The frontoparietal fontanelle is usually very widely exposed, sometimes slightly less so. Exposure is usually greater than shown in Fig. 14.

The exoccipital and prootic are never fused and dorsomedial and ventromedial ossification of the exocci-

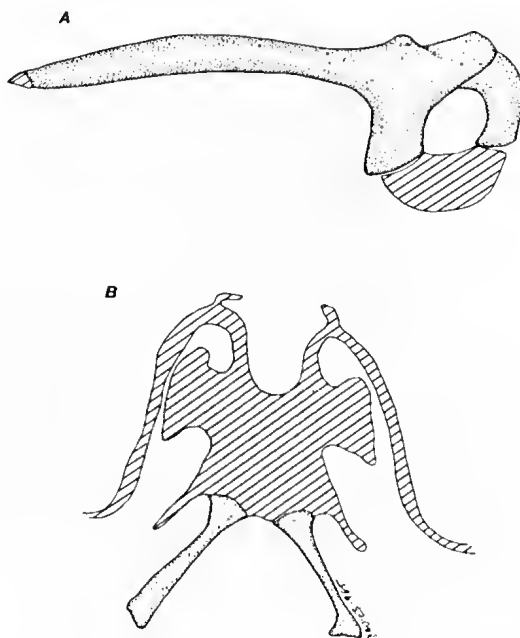


Fig. 13—*Uperoleia inundata* (UAZ B479). A, Lateral view of ilium. B, ventral view of hyoid.

pital is lacking. The crista parotica is always short and stocky and the epiotic eminences are prominent.

The condition of the zygomatic ramus of the squamosal varies. It is absent, tiny and straight, or tiny and knobbed. The otic ramus varies slightly in length: the usual condition is moderately long.

The palatines are expanded medially in about two-thirds of the specimens and unexpanded in the remainder. The cultriform process of the parasphenoid invariably is long and usually truncate. The alae are at right angles to the cultriform process; they are slender to moderately slender and vary slightly in length (Fig. 14).

The medial ramus of the pterygoid is usually very long and acuminate. Occasionally it is shorter and

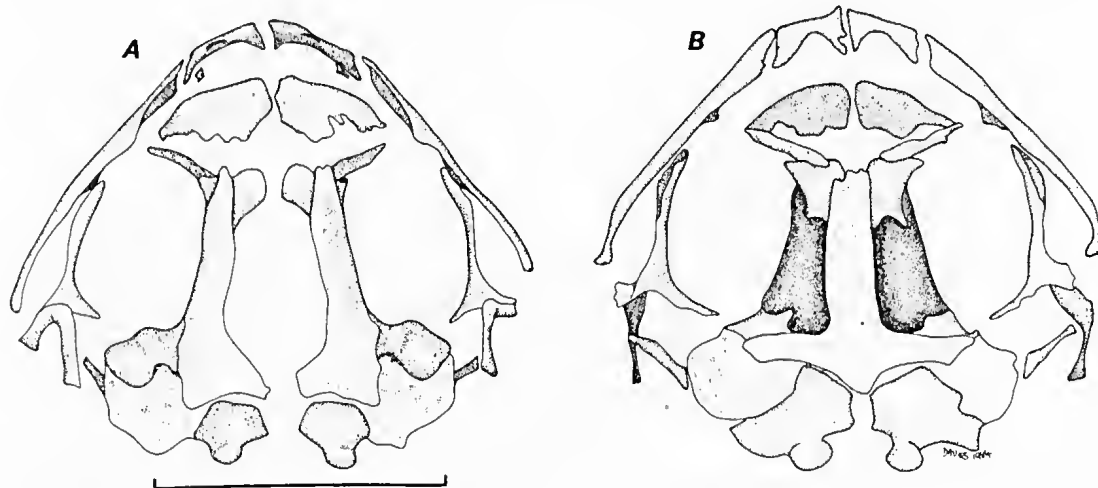


Fig. 14—*Uperoleia inundata* (SAM R25541). A, Dorsal and B, Ventral views of skull. Scale bar = 5 mm.

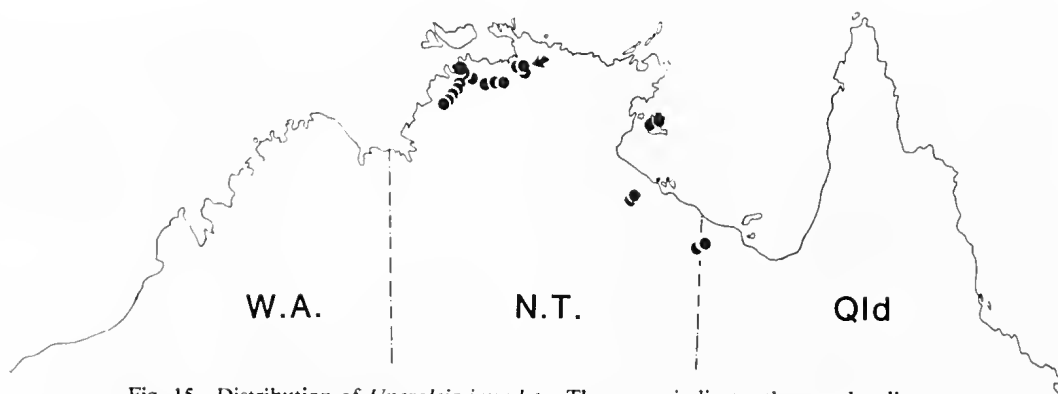


Fig. 15—Distribution of *Uperoleia inundata*. The arrow indicates the type locality.

aeuminate. The posterior process is usually broad, occasionally moderately acuminate. The anterior ramus is always in long contact with the maxillary.

The pars facialis of the maxillary varies slightly in depth. It is rarely shallow, and is usually moderately deep. The preorbital process is present, and usually well developed but can vary slightly in prominence.

The alary processes of the premaxillaries are inclined anteromedially. In one specimen (SAM R17268), they are unusually high. The palatine processes of the premaxillaries are usually moderately long and not closely applied; rarely, they are short.

The pterygoid process of the palatal shelf is usually poorly to moderately developed. Very rarely it is virtually absent (Fig. 14).

HABITAT: Males call from shallow water at the base of grass tussocks, under leaves and logs, from grass stems in water, and under leaf litter in sandy stream beds (Tyler *et al.* 1983, Tyler *et al.* 1986).

ADVERTISEMENT CALL: The call of *U. inundata* is a 'long call' of extreme variability. At least two calls are produced (Tyler *et al.* 1981a, Tyler *et al.* 1986).

LIFE HISTORY: Tyler *et al.* (1983) described the life history of this species and illustrated larval morphology including mouth disc structure.

DISTRIBUTION: *Uperoleia inundata* occurs in the north of the Northern Territory, on Groote Eylandt and on the western and southern coasts of the Gulf of Carpentaria. It penetrates into Queensland at the base of the Gulf of Carpentaria (collected at Westmoreland) (Fig. 15).

COMPARISON WITH OTHER SPECIES: *Uperoleia inundata* is an untoothed species with a widely-exposed frontoparietal fontanelle, features shared by *U. russelli*, *U. glandulosa*, *U. talpa*, *U. orientalis*, *U. crassa*, *U. borealis*, *U. arenicola* and *U. littlejohni*.

U. inundata may be distinguished from *U. russelli*, *U. crassa*, *U. talpa*, *U. orientalis* and *U. borealis* by poor toe webbing (absent or basal).

From *U. glandulosa* and *U. littlejohni*, *U. inundata* is distinguished by the absence of broad toe fringing and by the lack of strong dorsal patterning.

From *U. arenicola*, *U. inundata* is distinguished by greater ossification of the nasals.

Uperoleia trachyderma Tyler, Davies and Martin

Uperoleia trachyderma Tyler, Davies & Martin 1981, Trans. R. Soc. S. Aust. 105, p. 149.

Uperoleia trachyderma: Tyler, Davies & Martin 1983, p. 241; Cogger 1983, p. 87; Cogger, Cameron & Cogger 1983, p. 34; Tyler & Miller 1985, p. 45; Tyler 1985, p. 409; Tyler & Davies 1986, p. 60.

DEFINITION: A small to moderate-sized species (males 17–26 mm S-V) lacking maxillary teeth, with small eyes; toes broadly fringed; very small, rounded, outer metatarsal tubercle; widely-exposed frontoparietal fontanelle; dorsum covered with small conical tubercles; carpus of five elements; anteromedial processes of anterior hyale of hyoid slender; small ilial crest; call a staccato burst of four short pulses, with a pulse repetition rate of about 79 pulses sec⁻¹.

MATERIAL EXAMINED: N.T.: SAM R22336–48, Rankine River at Ranken Store, Alexandria Station; SAM R22325–35, Barkly Hwy, 500 m N Microwave Repeater 8502 Soudan Outstation, Alexandria Station; SAM R25952–61, 113.9 km S Victoria Hwy/Delamere Hwy Jen; SAM R24017, 415.1 km W Katherine on Victoria Hwy; SAM R24018–25, 4.4 km W Keep River (Newry Station) on Victoria Hwy.

Qld: QM J39012, Gunpowder Rd, 45.1 km E Mt Isa (20°23', 139°20'); QM J38969–72, J38975, 20 km E Cloncurry on Julia Creek Rd; QM J39089–91, 12.6 km E Camoweal on Barkly Hwy; QM J38965–8, 13.2 km E Cloncurry on Julia Ck Rd; QM J45955, SAM R29660–4, Lawn Hill Station.

EXTERNAL MORPHOLOGY: This species shows little morphological variation and is characterised by a fincly-tubercular dorsum (Tyler *et al.* 1981c), the texture of which has not been reported in any other Australian amphibian. Only males have been collected; those from western Qld are larger (21–26 mm S-V) than those from localities in the N.T. (17–23 mm S-V).

Hind limbs are moderately long [TL/S-V 0.35 ± .02, (0.31–0.39)] and eye to naris distance is always greater than internarial span [E-N/IN 1.35 ± .16 (1.07–1.83)]. The eye is consistently small, approximating eye to naris distance in the 56 specimens examined (Fig. 16).



Fig. 16—*Uperoleia trachyderma* in life (Alexandria Station, N.T.).

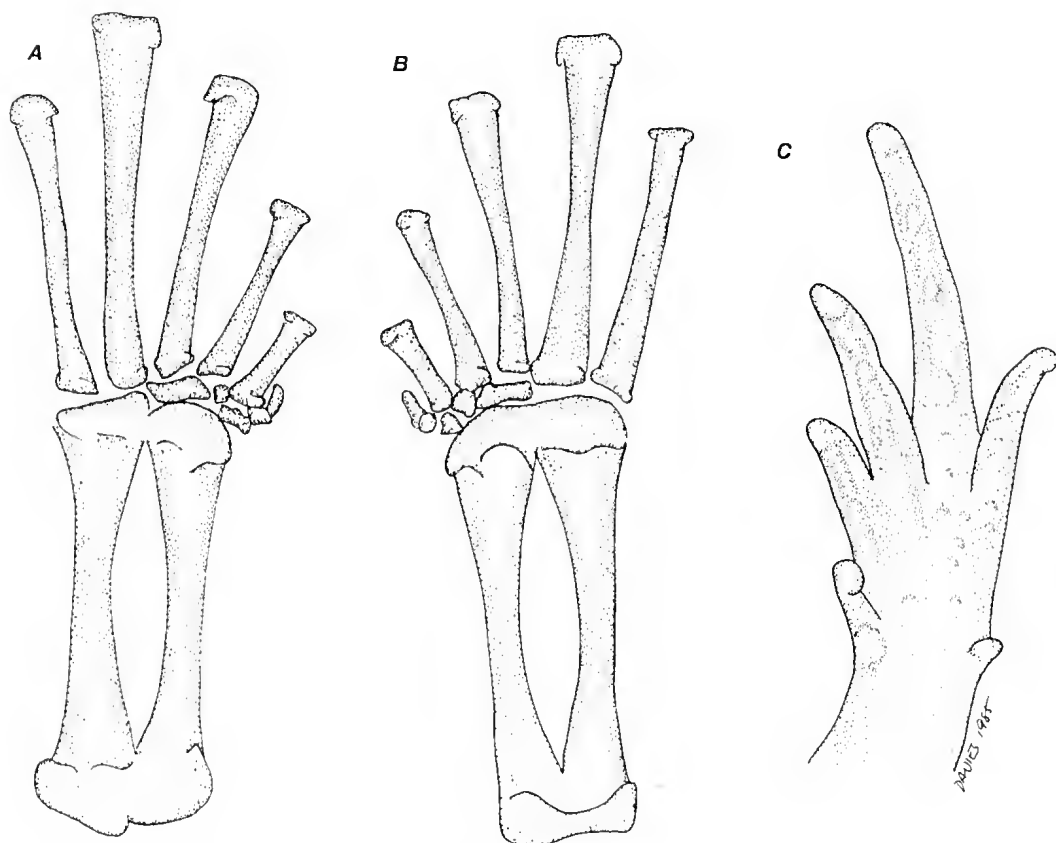


Fig. 17—*Uperoleia trachyderma*. A, Dorsal and B, Ventral view of tarsus (SAM R22331). C, Plantar view of foot (QM J38965).

Toes are well fringed; some specimens are unwebbed whilst others have basal webbing between the toes. Metatarsal tubercles are rounded and small. The inner is situated at the base of toe I and the outer is slightly angled to the long axis of the foot (Fig. 17C).

The characteristic tiny conical tubercles on the dorsal surface (Fig. 16) are restricted occasionally to the head and limbs, with only a trace on the dorsum.

Ventral pigmentation is not always as dense as reported in the type description. Dark stippling is exhibited in only some specimens and most have only a faint suffusion of pigment. In life, the frogs often have brilliant orange patches on the dermal glands (see Tyler & Davies, 1986, p. 50 for a colour illustration of this species) and they have a characteristic posture in which the head is depressed (Fig. 16).

OSTEOLOGY: Material examined: N.T.: SAM R22331, UAZ A621, A892-4, Barkly Hwy, 500 km N Microwave Repeater 8502, Soudan Outstation, Alexandria Station; UAZ A622, Rankine River at Ranken Store; UAZ A595-6, 113.9 km S Delamere Hwy/Victoria Hwy Jcn; UAZ A595, 4.4 km W Keep River on Victoria Hwy.

Here we supplement the type description with data on elements of the carpus, tarsus, pelvic girdle and hyoid.

Carpus: The carpus consists of five elements. Little torsion occurs. Both the O. ulnare and O. radiale are present. The O. radiale is the larger of the two. These elements articulate with the O. radioulna proximally and with each other on their proximomedial border. Distally both elements articulate with the large transversely-elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. preaxiale centrale (Fig. 18). The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. No flange is apparent on the lateroproximal corner of the O. centrale postaxiale. Ventromedially is a depression on which a palmar sesamoid is situated. The O. centrale preaxiale articulates laterally with the O. radiale and distally with the fused carpal elements of the O. distale carpale 2 and 3 and laterally with the basal prepollical element.

Tarsus: The O. tibiale and O. fibulare are elongated elements fused proximally and distally. The O. tibiale extends as far as the distal end of the O. fibulare. Three distal tarsal elements are present. The lateral element is the largest and lies at the base of O. metatarsus III. It extends laterally to articulate with the medioproximal side of the base of O. metatarsus II. The second element lies at the base, slightly laterally, to O. metatarsus II. The medial element lies at the base of O. metatarsus I, and articulates with the O. centrale prehallucis. The distal prehallucal element is small and slender (Fig. 17A, B).

Pelvic Girdle: A small proximal crest occurs on the ilium. The dorsal prominence is monticuline and supports a curved posterolateral protuberance (Fig. 19). The pubis is calcified.

Hyoid: The hyoid plate is about as broad as it is long. The alary processes are broad and not pedunculate. The anteromedial processes of the anterior hyale are slender and moderately long. The posterolateral pro-

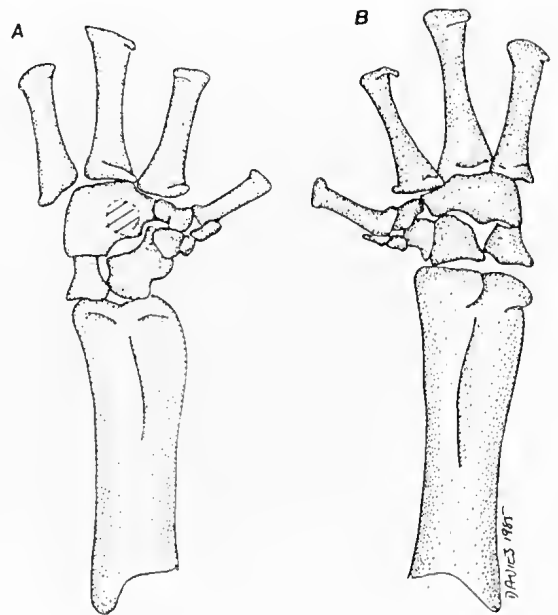


Fig. 18—*Uperoleia trachyderma* (SAM R22331). A, Ventral and B, Dorsal view of carpus.

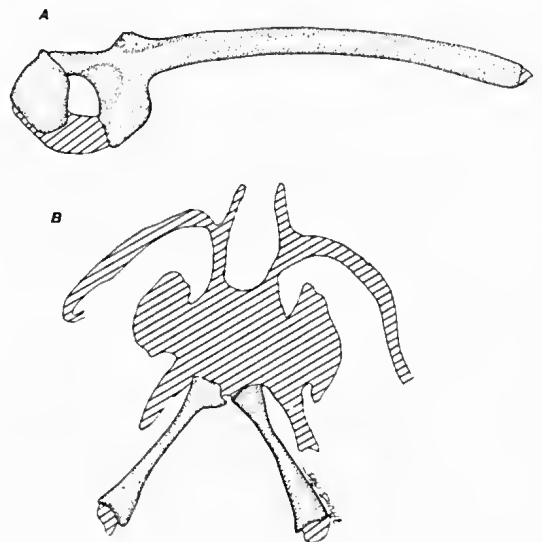


Fig. 19—*Uperoleia trachyderma* (SAM R22331). A, Lateral view of pelvis. B, Ventral view of hyoid.

cesses of the plate are moderately broad and moderately long. The posterior cornua are ossified (Fig. 19).

VARIATION: There is little variation in cranial osteology in the material examined. The nasals are very well ossified with slight variation in the degree of posteromedial separation. The nasals are always in tenuous contact with the sphenethmoid. The frontoparietal fontanelle is widely exposed and slight variation occurs in curvature of the orbital edges of the frontoparietal elements. Occasionally curvature is not detectable. The anterior extremities of the frontoparietals do not reach beyond the sphenethmoid.

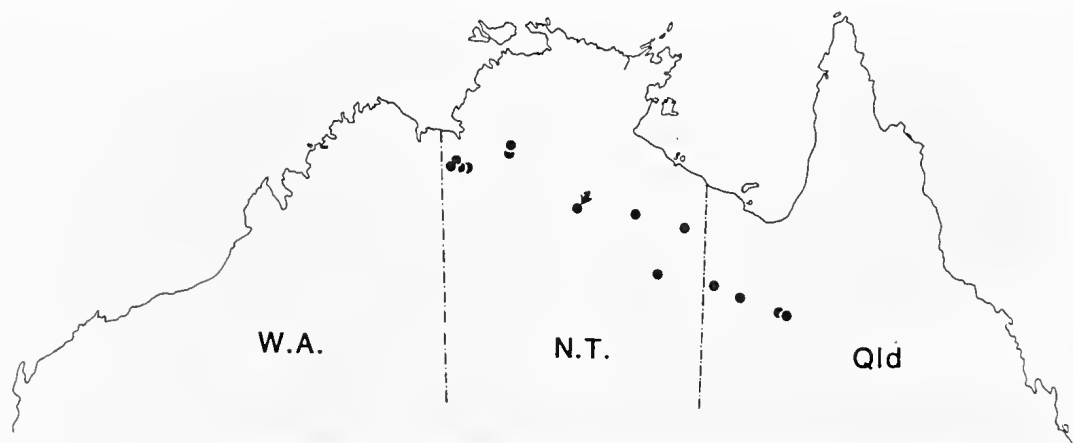


Fig. 20—Distribution of *Uperoleia trachyderma*. The arrow indicates the type locality.

The epiotic eminences are not prominent and posterior ossification appears to be complete, if thin. The zygomatic ramus of the squamosal is small but not bifid and some variation is found in length of the short otic ramus.

The maxillary and premaxillary are edentate and the pars facialis of the maxillary is shallow with a small preorbital process.

The palatines are acutely angled to the sphenethmoid, reduced laterally and do not extend beyond the truncated maxillary processes of the nasals. Vomerine fragments are present medial to the palatines in three specimens.

The anterior ramus of the pterygoid is in moderately-long contact with the moderately-prominent pterygoid process of the palatal shelf of the maxillary.

The cultriform process of the parasphenoid is broad in this species and the alae are short and angled slightly posterolaterally.

The distal carpal 2 and 3 are fused in all specimens.

ADVERTISEMENT CALL: Tyler *et al.* (1981c) reported the advertisement call of *U. trachyderma* from the type locality as a harsh 'creak' of four short pulses with a pulse repetition rate of about 79 pulses sec⁻¹.

DISTRIBUTION: *Uperoleia trachyderma* is confined to the grey self-mulching cracking clays (Northcote *et al.* 1975) of the Northern Territory and western Queensland (Fig. 20). *U. trachyderma* is the only species within *Uperoleia* that can be associated with a particular soil type (Tyler, Davies, Watson, Martin unpubl., Tyler & Davies 1986). **COMPARISON WITH OTHER SPECIES:** *Uperoleia trachyderma* is an untoothed species with a widely-exposed frontoparietal fontanelle, features shared by *U. russelli*, *U. talpa*, *U. glandulosa*, *U. crassa*, *U. borealis*, *U. orientalis*, *U. inundata* and *U. arenicola*.

From *U. russelli*, *U. talpa*, *U. crassa*, *U. borealis*, *U. glandulosa* and *U. orientalis*, *U. trachyderma* is distinguished by the absence of webbing or presence of only basal webbing on the toes. From *U. inundata* and *U. arenicola*, *U. trachyderma* is distinguished by the presence of broad fringes on the toes and a tiny conical

outer metatarsal tubercle (broad and elevated in the former two species).

Uperoleia capitulata sp. nov.

HOLOTYPE: QM J26428, an adult male collected at Bollon, Queensland (28°02', 147°29') on 22.viii.1975 by G. Czechura.

DEFINITION: A moderate-sized species (males 19–27 mm S-V, females 27–28 mm S-V) with a tiny head; relatively smooth dorsum; hypertrophied dermal glands; maxillary teeth absent; frontoparietal fontanelle poorly exposed; no webbing between the toes; outer metatarsal tubercle rounded and angled moderately acutely to the long axis of the foot; carpus of five elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent. Call not known.

DESCRIPTION OF HOLOTYPE: Maxillary teeth absent. Vomerine teeth absent. Snout short, truncated when viewed from above and rounded in profile (Fig. 22). Eye to naris distance greater than internarial span (E-N/IN 1.40). Canthus rostralis inconspicuous and straight. Tympanum not visible externally (Fig. 22). Head small in relation to body (Fig. 22). Fingers long, slender, fringed and unwebbed with prominent subarticular tubercles (Fig. 22). In order of length, 3 > 4 > 2 > 1. Palmar tubercles prominent, that at base of thumb less conspicuous. Hind limbs short (TL/S-V 0.36). Toes long, moderately fringed, unwebbed with conical subarticular tubercles (Fig. 22). Inner and outer metatarsal tubercles prominent, raised; inner gently rounded, aligned along axis of, and encroaching upon, digit 1; outer rounded, angled moderately acutely to axis of foot. Toes in order of length 4 > 3 > 5 > 2 > 1.

Dorsal surface smooth with hypertrophied parotoid, inguinal and coccygeal glands. Submandibular gland discrete, displaced to anterior face of hypertrophied parotoid gland. Finely-fimbriated supracloacal flap. Ventral surface smooth.

Male with unilobular submandibular vocal sac. In preservative, dorsal surface grey with darker chocolate markings. Parotoid, inguinal and coccygeal glands with cream markings. Ventral surface cream with faint



Fig. 21 — *Uperoleia capitulata* sp. nov. from Charleville, Qld (SAM R29593).

dusting of patches of chocolate pigment granules. Pale patches in groin and post femoral regions.

COLOUR IN LIFE (based on SAM R29593): Ground colour grey with well-defined dark grey patches upon the head, scapulae, mid dorsum, and coccygeal region, and narrow transverse bars across the limbs. Faint spectrum orange (Smithe 1975) spots upon the parotoid, inguinal and coccygeal glands and on tips of some small dorsal tubercles. Ventrally whitish with faint brown stipples just behind pectoral region, and on flanks. Throat grey with fine white stipples in male. Pectoral region and ventral thighs unpigmented. Inguinal and femoral patches flame scarlet.

DIMENSIONS (in mm): Snout-vent length 23.8; tibia length 8.5; cyc diameter 2.2; eye-naris distance 2.1; internarial span 1.5.

VARIATION: There are 27 paratypes, 20 ♂♂ 3 ♀♀ and 4 subadults.

Qld: QM J26427, taken with the holotype; J39196, Byanda Station, 20 km WNW Proston, T. Pulsford, 11.i.1981; QM J26416, 1 km N Thargomindah, G. Ingram *et al.*, 24.viii.1975; SAM R29586-7, QM J45960, CAS 160141, 64 km SW Bulloo Downs Hstd, D. G. McGreevy, S. Tickler, 2.x.1976; SAM R29588, QM J45956, Noccundra Hotel, K. R. McDonald, D. G. McGreevy, 30.xi.1975; QM J45957-8, SAM R29590, Boorara Station, 32 km N Hungerford, S. May, late 1976; SAM 29589 Boorara Station, D. G. McGreevy 12.i.1977; SAM R29591, KU 205026, King Tank, Ambathala Nature Reference Site (26°00', 145°00'), K. R. McDonald, D. G. McGreevy 3.v.1979; SAM R29592-5, QM J45959, DPI Swamp, Charleville, P. D. McRae, 10.ii.1986.

N.S.W.: AM R24474, R24479, R24481, R24488, R24492, Nyngan, H. G. Cogger, 11.i.1964; AM R28636-7, between Nyngan and Nevertire, W. McCreddie, 6.xi.1969.

All paratypes are small-headed, robust specimens with bold dorsal patterning of chocolate on a grey and brown background, and cream dermal glands. Males range from 19-27 mm, females 27-28 mm. Hind limbs are relatively long [TL/S-V $0.37 \pm .02$ (♂♂ $0.34-0.40$, ♀♀ $0.31-0.36$)]. Eye to naris distance is greater than internarial span [E-N/IN $1.36 \pm .25$ (1.1-2.08)].

Ventral patterning is better developed in some paratypes, but is never more than patches of brown pigment on the anterior half of the body. The dorsum is faintly or moderately rugose in some specimens (Fig. 21) and hypertrophy of the dermal glands is not always as acute as in the holotype. The snout is sometimes more rounded. Toes rarely show greater fringing than described. The inguinal and post-femoral, light-coloured patches are often more obvious than in the holotype. A pale stripe occasionally occurs in the midline of the head.

OSTEOLOGY (based on SAM R29586): Skull moderately ossified, sloping anteroventrally. Ossification of sphenethmoid incomplete medially; anterior extremities not extending anteriorly to frontoparietals dorsally; extending about $\frac{1}{3}$ posteriorly on length of orbit in ventral view. Prootic not fused with exoccipital. Exoccipital not confluent dorso- or ventromedially. Crista parotica short, stocky, not articulating with otic ramus of squamosal. Very shallow groove of carotid canal on frontoparietals medial to epiotic eminences. Frontoparietal fontanelle poorly exposed, overlain by medially-crenate frontoparietals (Fig. 23) extending entire length of orbit. Anterior margin of fontanelle formed by sphenethmoid at level about $\frac{1}{4}$ posteriorly on length of orbit. Posterior margin undefined because of absence of medial prootic ossification.

Nasals large, approximately triangular, projecting ventrally at lateral extremities, and with slightly-concave anteromedial edge (Fig. 23). Poorly separated medially except for posterior $\frac{1}{4}$ where slight increase in separa-

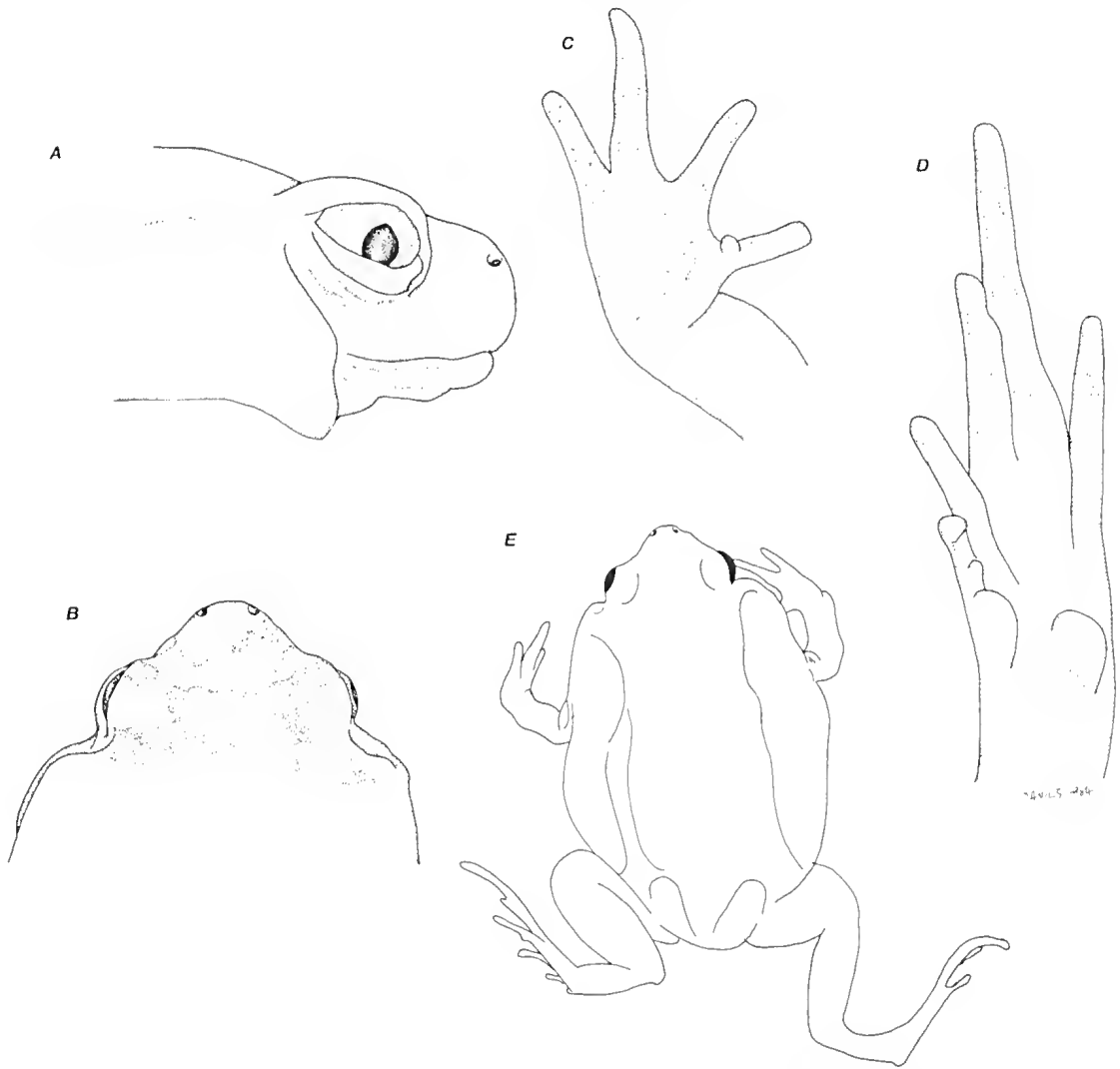


Fig. 22—*Uperoleia capitulata* sp. nov. (holotype). A, Lateral and B, Dorsal views of head. C, Palmar view of hand. D, Plantar view of foot. E, Dorsal view of frog showing hypertrophied glands.

tion present; not in bony or tenuous contact with sphenethmoid or with anterolateral extremities of frontoparietals. Maxillary process of nasal not developed—lateral extremity truncate, widely separated from shallow pars facialis of maxillary which lacks a pre-orbital process.

Palatines moderately robust, not extending laterally beyond lateral extremities of nasals; very slightly expanded medially, overlying anterior extremities of sphenethmoid along posterior half of proximal third of element (Fig. 23). Parasphenoid robust; cultriform process moderately broad, truncate, reaching anterior edge of sphenethmoid. Alary processes short, moderately broad, not overlain by medial rami of pterygoid. Medial rami of pterygoid short, robust, not in bony contact with prootic region; posterior rami short, broad; anterior rami in long contact with well-developed pterygoid process of palatal shelf of maxillary.

Cartilaginous quadrate present between base of squamosal and quadratojugal. Quadratojugal robust and in firm contact with maxillary. Squamosal shaft robust, zygomatic ramus extremely short; otic ramus moderately long and slender, unexpanded. Maxillary and premaxillary edentate. Palatal shelf moderately deep with well-developed palatine processes, poorly separated medially, and with well-developed pterygoid processes.

Alary processes of premaxillaries slender, inclined medially and slightly anteriorly. Vomers absent. Bony columella present. Pectoral girdle arciferal and robust. Omosternum absent, xiphisternum present. Sternum cartilaginous. Clavicles very slender, curved, closely applied medially. Coracoids moderately robust, widely separated medially, Scapula biapitate, slightly shorter than clavicles. Suprascapula about $\frac{1}{2}$ ossified.

Eight non-imbricate presacral vertebrae. Sacral

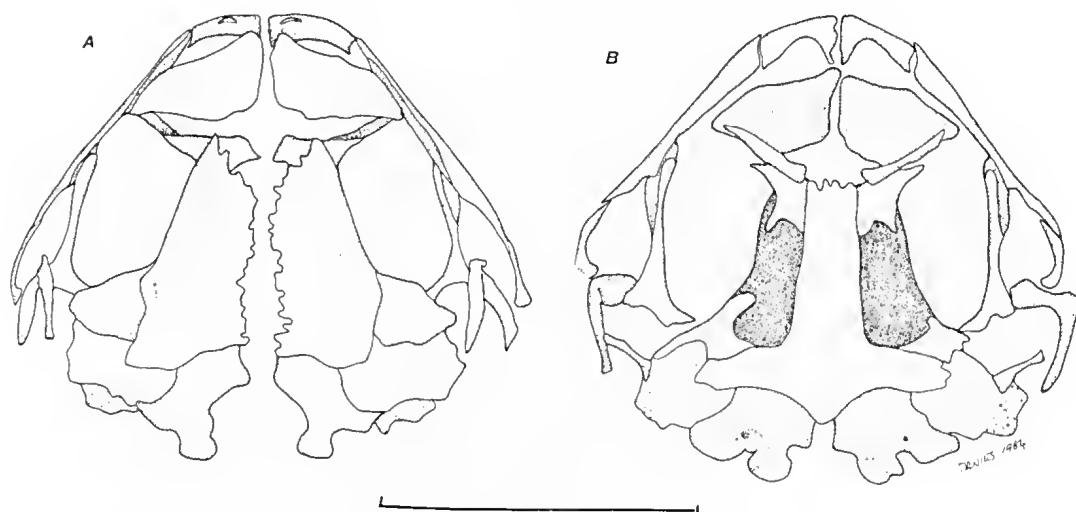


Fig. 23—*Uperoleia capitulata* sp. nov. (SAM R29586). A, Dorsal and B, Ventral views of skull. Scale bar = 5 mm.

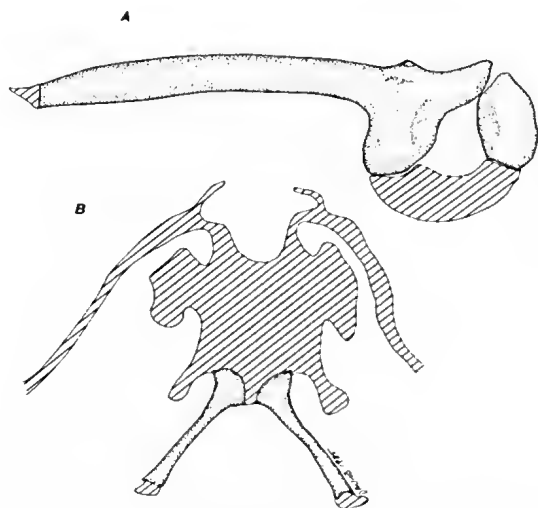


Fig. 24—*Uperoleia capitulata* (QM J45960). A, Lateral view of the pelvic girdle. B, ventral view of the hyoid.

diapophyses poorly expanded. Relative widths of transverse processes $\text{III} > \text{II} = \text{sacrum} = \text{IV} > \text{V} > \text{VI} = \text{VII} = \text{VIII}$. Bicondylar sacrooocygeal articulation on urostyle. Well-developed crest extending $\frac{2}{3}$ length of urostyle. No ilial crest; dorsal prominence small, montieuline; dorsolateral dorsal protuberance (Fig. 24). Pubis calcified.

Humerus with strongly-developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3. Carpus with five elements. Moderate torsion; O. radiale and O. ulnare present; O. radiale larger. Both elements articulate with O. radioulna proximally, with each other proximomedially and with large, transversely-elongate O. centrale postaxiale distally. O. radiale articulates laterally with O. centrale preaxiale (Fig. 25). O. centrale postaxiale articulates distally with bases of O. metacarp

III, IV and V. Small flange extends proximally from lateroproximal corner. Palmar sesamoid ventromedially (Fig. 25). O. centrale preaxiale articulates laterally with O. radiale, distally with O. centrale postaxiale and with fused carpal elements of O. distale carpal 2 and 3, and laterally with basal prepollical elements. Distal tips of terminal phalanges knobbed.

Phalangeal formula of foot 2,2,3,4,3. O. tibiale and O. fibulare elongate and fused at either end. O. tibiale extends to distal end of O. fibulare. Three distal tarsal elements present. Lateral element largest, lying at base of O. metatarsus III extending laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Second element lies at base and slightly laterally to O. metatarsus II. Medial element lies at base of O. metatarsus I, articulating also with O. centrale prehallucis. Distal prehallucal element elliptic, extending approximately $\frac{1}{3}$ length of O. metatarsus I (Fig. 25).

Hyoid plate slightly longer than broad. Antero-medial processes of anterior hyale short and slender (Fig. 24). Alary processes of hyoid plate not pedunculate. Posterolateral processes moderately broad, moderately long. Posterior cornua ossified.

VARIATION: A further five paratypes have been cleared and stained; QM J545960, J45958, SAM R29587, QM J26416, AM R28637.

The nasals are in tenuous contact with the sphenethmoid in AM R28637 and QM J45958. The exposure of the frontoparietal fontanelle varies slightly in the paratypes. Exposure is never less than shown and is sometimes greater. In QM J26416 exposure is increased by contraction of the frontoparietals about $\frac{2}{3}$ along their length posteriorly.

The pars facialis of the maxillary is slightly deeper than in SAM R29586 in all the other skeletons. The palatines are not expanded medially other than in QM

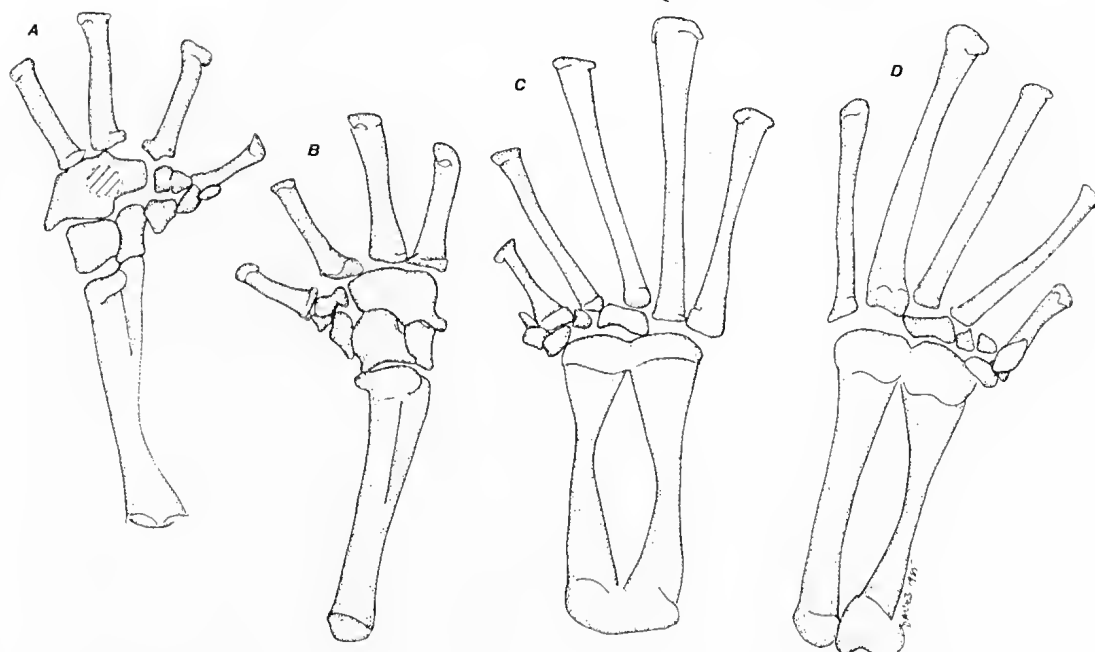


Fig. 25 — *Uperoleia capitulata* sp. nov. (SAM R29586). A, Ventral and B, Dorsal views of carpus. C, Ventral and D, Dorsal views of tarsus.

J26416. Vomcrine fragments are present medial to the palatines in SAM R29587.

HABITAT: Found in mulga woodland at Ambathala Nature Reference Site and in coolibah (*Eucalyptus microtheca*) lined waterholes at Noccundra.

ADVERTISEMENT CALL: The advertisement call of this species is not yet known.

COMPARISON WITH OTHER SPECIES: *Uperoleia capitulata* is an untoothed species with a poorly-exposed frontoparietal fontanelle, features shared by some *U. lithomoda* and by *U. mimula*.

From *U. lithomoda* and *U. mimula*, *U. capitulata* is distinguished by its hypertrophied paratoid glands and relatively-smooth dorsum.

From the sympatric untoothed species *U. rugosa*, *U. capitulata* is distinguished by its hypertrophied dermal glands and greater exposure of the frontoparietal fontanelle.

DISTRIBUTION: *Uperoleia capitulata* is confined to south western Qld and northwestern N.S.W., particularly in the Bulloo drainage system (Fig. 26). *U. capitulata* is sympatric with *U. rugosa* at some localities.

ETYMOLOGY: From the Latin *capitulus* meaning having or ending in a small head, alluding to the characteristic feature of this species.

COMMENT: *Denisonia devisi* was observed feeding on this species at Range Tank, Ambathala Nature Reference Site.

Uperoleia fusca sp. nov.

Uperoleia marmorata: Moore 1961, p. 219 (part.);

McDonald 1974, p. 2; Czechura 1978, p. 150;

McEvoy, McDonald & Searle 1979, p. 176.

Uperoleia laevigata: Ingram & Corben 1975, p. 49.

Uperoleia sp.: Webber & Cogger 1976, p. 76; Thompson 1981, p. 94.

HOLOTYPE: SAM R29596, an adult male collected adjacent to southern boundary of Eungella N.P., 1.2 km along Credition road from Broken River Crossing Qld (148°30'10", 21°10'15"), by M. J. Tyler and K. R. McDonald on 26.i.1984.

DEFINITION: A moderate-sized species (males 20-28 mm S-V, females 23-29 mm S-V) with a smooth dorsum; maxillary teeth present; toes unwebbed; frontoparietal fontanelle unexposed; ventral surface entirely pigmented; carpus of six elements; anteromedial processes of anterior hyale of hyoid in form of medial thickening; ilial crest absent; call a rasping note of about 20 pulses.

DESCRIPTION OF HOLOTYPE: Maxillary teeth present. Vomerine teeth absent. Snout moderately short, rounded when viewed from above (Fig. 27), gently sloping posteriorly in profile (Fig. 27). Eye to naris distance very slightly greater than internarial span (E-N/IN 1.1). Nares dorso-laterally positioned. Canthus rostralis inconspicuous and straight. Loreal region straight. Tympanum not visible externally. Fingers moderately long, slender, unfringed, unwebbed with moderately-prominent subarticular tubercles but obscure palmar tubercles. In order of length $3 > 4 > 2 > 1$ (Fig. 27). Hind limbs moderately long (TL/S-V 0.40). Toes long, very poorly fringed and unwebbed (Fig. 27). In order of length $4 > 3 > 5 > 2 > 1$. Metatarsal tubercles small, inner rounded and flattened on axis of toe 1, outer small and conical, moderately acutely angled to the long axis of the foot. Subarticular tubercles small, not very prominent.

Dorsal surface faintly rugose (Fig. 28). Parotoid glands moderately developed, inguinal and coccygeal

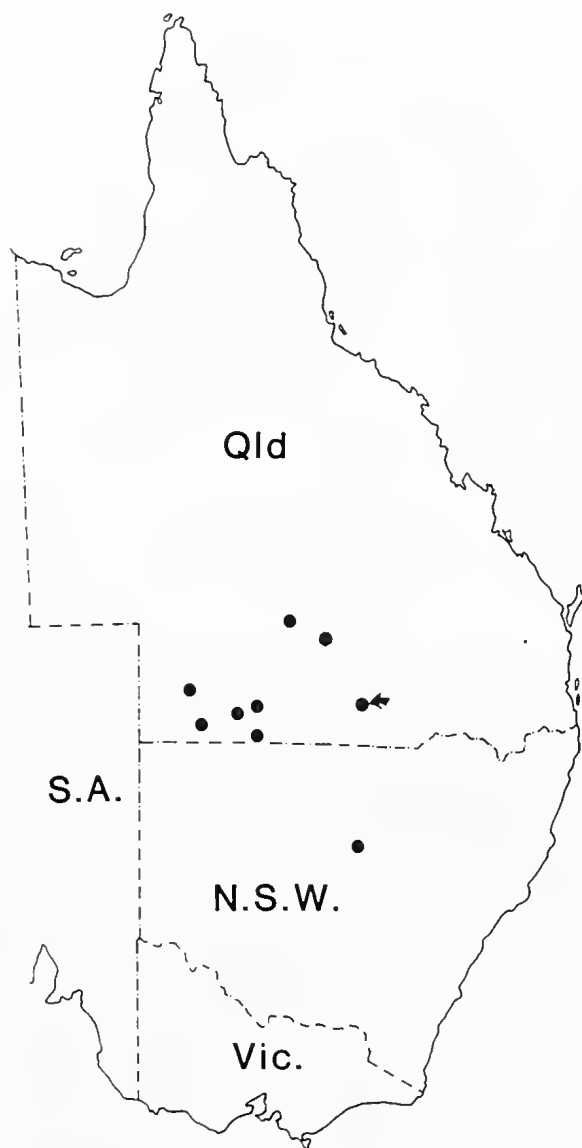


Fig. 26—Distribution of *Uperoleia capitulata* sp. nov. The arrow indicates the type locality.

glands not obvious. Submandibular gland disrupted. Cloacal flap with short fimbriations. Flap in anterior corner of eye. Ventral surface smooth.

Male with unilobular submandibular vocal sac. Dorsum grey in preservative with black and cream mottling. Entire ventral surface, including femoral regions pigmented with chocolate coloured patches of granules. Palmar surface of hand moderately pigmented, plantar surface of foot heavily pigmented. Throat darkly pigmented with paler diamond shaped patch at mandibular symphysis. Small, palc, post-femoral patch. Colour in groin and post-femoral patches reddish/orange in life. Nuptial pad unpigmented (Fig. 29).

DIMENSIONS (in mm): Snout-vent length 23; tibia length 9.3; eye diameter 2.9; eye-naris distance 2.0; internarial span 1.9.

VARIATION: There are 199 paratypes, 192 ♂♂ and 7 ♀♀.

N.S.W.: SAM R12590(12), Wyong, 1.6 km S, 9.6 km W of Ulong, F. Parker, H. Ehmann, P. Krauss, 26.i.1971; AM R15505-6, Boolamboyle, R. Mackay; AM R104374, R101331, 11 km from jcn with Pacific Hwy on Palm Grove Rd, Ourimbah, H. G. Cogger, 3.xi.1981; AM R4631-2, Worrell Ck, Nambucca River, W. Clark, 24.i.1910; AM R6301-2, Garavambi near Macksville on Nambucca River (30°44', 152°59'), D. B. Fry and H. E. Smart, 1913; AM R53987-93, R53995-6, Erina, N. Dankers, 1974; AM R68438, 24.5 km N Colo Heights, Putty Rd (33°13', 150°40'), P. Rankin and P. Greer, 15.xi.1975; AM R70200, 12.8 km along road to Wisemans Ferry from Kariong, R. Wellington, 25.i.1978; AM R115583 Whitman Creek, S. J. Copland, 6.i.1948; NMV D25047-8, D25056-7, Ourimbah Creek, M. J. Littlejohn, A. A. Martin, P. A. Rawlinson, 1.xi.1964; SAM R29597-8, same locality, M. Mahony, 3.xi.1981; AM R76508, same locality, D. O'Brien; NMV D25049-55, 10.4 km S Gloucester, M. J. Littlejohn, A. A. Martin, P. A. Rawlinson, 29.x.1964; NMV D43207-10, 2.6 km N Coff's Harbour, G. F. Watson, D. F. Gartside, 11.xi.1972; NMV D25044-6 Nymboida, M. J. Littlejohn, 27.x.1964; NMV D43223, 17.6 km S Grafton, G. F. Watson, D. F. Gartside, 8.xi.1972; NMV D43247-8, D42679, D42681, 4.8 km SE Lower Creek on Kempsey-Armidale Rd, G. F. Watson, D. F. Gartside, 12.xi.1972; QM J40431, J40435, Undercliff, G. Czechura.

Qld: SAM R29599-602, QM J45961, collected with the holotype; SAM R29603-7, same locality, K. R. McDonald, 5.i.1976; KU 205027-8, same locality, K. R. McDonald, 4.ii.1975; AMNH 124732, same data, 28.i.1975; QM J31556-62, J31582 Eungella, C. Corben; AM R53809-11, 16 km S Eungella (21°17', 148°36'), J. Barker, G. Grigg, 30.xii.1973; SAM R29608-11, QM J45962, CAS 160142-3, MCZ 108612-3, Bellthorpe S.F. (26°44', 152°36'), K. R. McDonald, J. S. McEvoy, D. G. Crossman, 27.ii.1976; BMNH 1986.203, same locality, K. R. McDonald, P. Amos, 24.xi.1976; SAM R29612-3, same locality, K. R. McDonald, Jan. 1979; QM J45963-65, Jimna Rd nr Yello turnoff, Sunday Creek S.F., K. R. McDonald, J. S. McEvoy, 5.i.1977; SAM R29614-6, Crows Nest N.P., K. R. McDonald, 14.i.1974; SAM R29617, Mt Glorious, C. J. Limpus, K. R. McDonald, 20.ii.1974; SAM R29618, 2 km from Sunday Creek turnoff along Jimna/Bellthorpe Rd (152°29', 26°42'), K. R. McDonald, 13.xii.1978; SAM R29619, Moreton Is., nr Blue Lagoon swamp, K. R. McDonald, 16.ix.1976; QM J10901-2, Mt Nebo, S. Breedon, Feb. 1961; QM J10900, J12309, J12294, J12323, same data, 19.ii.1964; QM J42609, J42576, J42614, below Bombana N.P., Mt Nebo Rd (27°24', 152°47'), C. Corben, A. Smyth, 31.x.1973; QM J19942, J19947, J19952, J19965, Dunwich, North Stradbroke Is., I. R. Straughan; QM J24088, Brown Lake, North Stradbroke Is., G. Ingram, G. Czechura, 5.iv.1974; QM J27563, Blue Lake, North Stradbroke Is., D. Grace, 2.i.1976; QM J27905, same locality, A. Elliot, M.

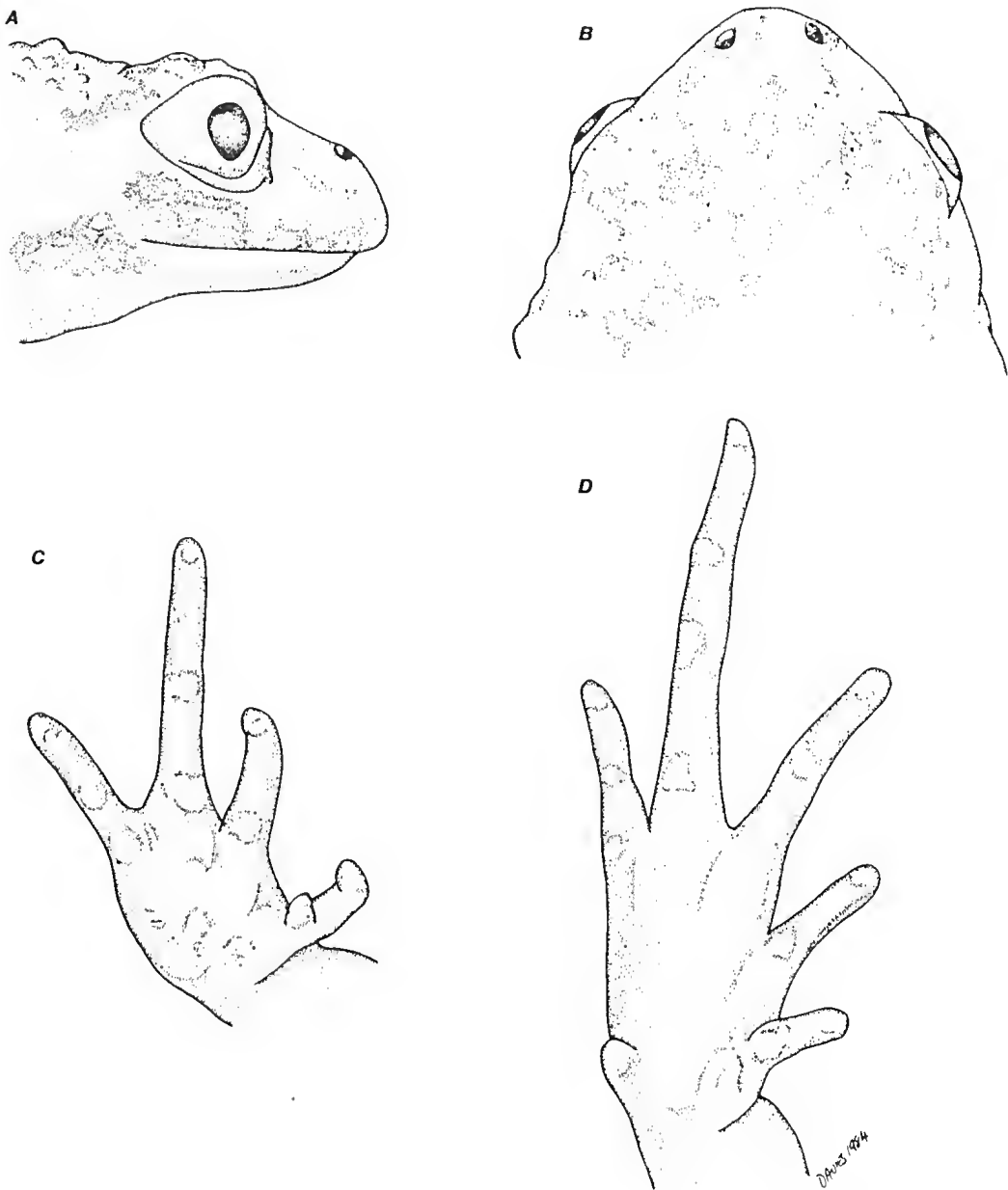


Fig. 27—*Uperoleia fusca* sp. nov. (holotype). A, Lateral and B, Dorsal view of head. C, Palmar view of hand. D, Plantar view of foot.

Hillier, 10.v.1976; QM J40020, Tortoise Lagoon, Blue Lake area ($21^{\circ}08'$, $148^{\circ}29'$), L. Kading, 22.x.1981; QM J42569, J42572, J42583, J42606-7, Brown Lake, North Stradbroke Is., C. Corben *et al.*, 8.ix.1973; QM J42593, same data, 15.ix.1973; QM J19925, J19927, J19930, J19936, J19959, J19961, J19966, Slacks Creek, Pacific Hwy, I. R. Straughan, 9.x.1961; QM J40433, Cooloola, G. Czechura, 1.i.1974; QM J27477, J27475, Lake Cooloomera, Cooloola, C. Corben, A. Smyth, 21.xi.1973; QM J42586-90, QM J42610, J42612, same locality, G. Ingram, 14.vii.1973; QM J27481, same locality, G. Ingram, G. Czechura, 30.xii.1973; QM

J42564, J42566-68, J42574-5, J42578-9, J42581, J42585, J42591-2, J42594, J42596, J42599-603, J42611, same locality, C. Corben *et al.*, 15.ix.1973; QM J39315, Poona Lake, Cooloola N.P., G. Monteith, Jan. 1981; QM J42565, J42570-1, J42573, J42580, J42584, J42595, J42604-5, J42608, J42613, Lost World ($28^{\circ}15'$, $153^{\circ}07'$), C. Corben *et al.*, 28.vii.1973; QM J42563, J42597-8, J42582, Calam Rd, Runcorn ($27^{\circ}36'$, $153^{\circ}04'$) C. Corben, G. Ingram, 10.x.1973; QM J40434, Maleny, G. Czechura, Feb. 1974; QM J40489-90, same data, 13.iv.1974; QM J40486-7, same data, April 1974; QM J40484, same data, 26.ix.1974; QM J41533, Pine Creek



Fig. 28—*Uperoleia fusca* sp. nov. in life (Topotype).



Timber Reserve south of 'Turkey' nr Miriamvale, T. Pulsford, 10.i.1983; QM J19938, J19953, J19957, Mt Tamborine, I. R. Straughan, 27.ix.1964; QM J18817, J18825, Moggill Rd, 8 km past Kenmore P.O., Brisbane, I. R. Straughan and A. K. Lee, 26.i.1961; QM J18837, Gold Creek Rd, 1.6 km past Brookfield turnoff, Brisbane, A. K. Lee, 26.ii.1961; QM J18822, Sampsonvale, A. K. Lee, 13.viii.1961; QM J29280, Kilcoy, G. Czechura, Nov. 1976; QM J19956, Warrawee, I. R. Straughan, 1.iii.1964; QM J19939, J19941, Brookfield Showground, Moggill Rd, Brisbane, A. K. Lee, 9.x.1961; QM J19943, 16 km N Gayndah, I. R. Straughan, 17.x.1963; QM J40315, Deepwater Rd, south of township '1770', T. Pulsford, 1.iv.1972; QM J30606, Ravensbourne, R. Sadlier, 7-8.i.1978; QM J18832, 3.2 km N Tamborine Village on Tamborine-Waterford Rd, I. R. Straughan, 12.ix.1964; QM J12721, Eidsvold, T. L. Bancroft, 30.viii.1912; QM J19958, 16 km N Cooroy, I. R. Straughan, 17.x.1963; AM R47734, R47736-7, Eurimbula E of Miriamvale, P. Webber.

Many of the male paratypes exhibit well-defined glandular, unpigmented nuptial pads (Fig. 29). Pigmentation of the ventral surface of the hands makes the pads particularly prominent in this species. Paratypes are all long-legged frogs [TL/S-V $0.38 \pm .02$, (0.35-0.42)]. Eye to naris distance approximates internarial span in most paratypes [E-N/IN $1.18 \pm .17$, (0.88-1.67)]. The gentle

Fig. 29—Palmar view of hand of *Uperoleia fusca* sp. nov. showing unpigmented subepidermal nuptial pad (SAM R29618).

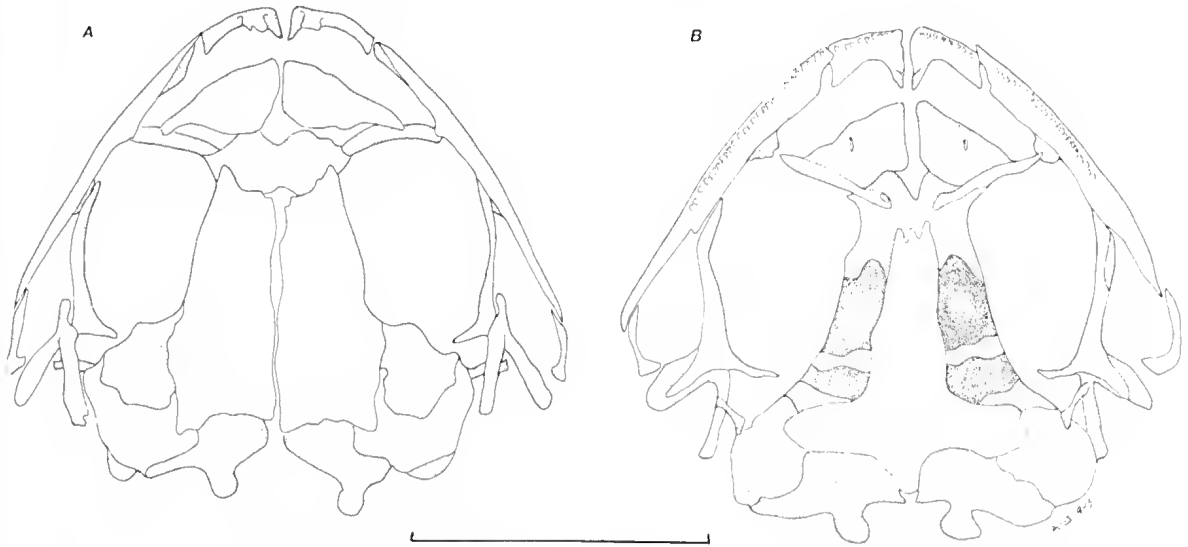


Fig. 30—*Uperoleia fusca* sp. nov. (SAM R29603). A, Dorsal and B, Ventral views of skull. Scale bar = 5 mm.

posterior slope of the snout of the holotype in lateral view, is characteristic of all paratypes.

All but three of the paratypes lack a distinct palmar tubercle at the base of the thumb. In the exceptions, the tubercle is better defined, but not prominent. Only four paratypes have toe fringing greater than in the holotype.

Dorsal patterning varies; some specimens are uniformly dark slate and others have bold chocolate patterning on a grey or brown background; many specimens exhibit an indistinct triangular preocular patch characteristic of the other toothed eastern Australian congeners. A pale midvertebral stripe occurs occasionally and many paratypes exhibit heavier ventral pigmentation than the holotype. Ventral pigmentation ranges from faint suffusions on a cream background to light speckles on a chocolate or slate background. Fading of pigmentation in preservative is common in this genus. Of the specimens with lighter ventral pigmentation, the pigment is spread uniformly across the entire ventral surface.

In life there is a dichotomy in inguinal and post-femoral colour. Where recorded (AM R6302, NMV D43247-8, SAM R29608-11) thigh colour at the southern part of the range of the species is yellow but in the northern part of the range is reddish/orange. Both thigh colours were recorded in specimens calling at a pool in the Conondale Ranges (SAM R29608-9, yellow thighed and SAM R29610-11 reddish/orange). The calls of these two forms were indistinguishable to the ear (K. R. McDonald unpubl.) and there are no morphological distinctions between the four specimens.

OSTEOLOGY (based on SAM R29603): Skull well ossified, sloping slightly anteroventrally. Ossification of sphenethmoid complete medially, dorsally extends to posterior extremities of nasals, ventrally extends about $\frac{1}{3}$ length of orbit posteriorly. Prootic not fused with exoccipital (Fig. 30). Epiotic eminences prominent. Exoc-

cipital not ossified dorsomedially or ventromedially. Crista parotica short, stocky, not articulating with long otic ramus of squamosal. Shallow groove for carotid canal present posteriorly on frontoparietals. Frontoparietal fontanelle exposed only as a median slit between the well-ossified frontoparietal elements. Anterior extremity about level of anterior ramus of pterygoid. Posterior extremity undefined.

Nasals moderately ossified, triangular, closely applied medially with slight separation posteriorly (Fig. 30); in tenuous contact with sphenethmoid. Maxillary process of nasal poorly developed, not in bony contact with well-developed preorbital process of shallow pars facialis of maxillary. Palatines moderately broad, slightly reduced and truncated laterally from level of dorsal extremity of preorbital process of pars facialis of maxillary (Fig. 30); angled at about 45° to overlay sphenethmoid medially.

Parasphenoid robust. Cultriform process moderately broad, not reaching level of palatines. Alae robust, deep, not angled to cultriform process; not overlapped nor reaching extremity of medial ramus of pterygoid. Medial ramus of pterygoid slender, acuminate, not in bony contact with prootic region. Posterior ramus moderately long, slender; anterior ramus in moderately-long contact with moderately-developed pterygoid process of palatal shelf. Small cartilaginous quadrate present at base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Squamosal shaft robust, short, knobbed, zygomatic ramus, long unexpanded otic ramus.

Maxillary and premaxillary dentate. Palatal shelf moderately deep with well-developed palatine processes, not abutting medially, and poorly- to moderately-developed pterygoid process. Alary processes of premaxillaries moderately slender, poorly bifurcated dorsally, slightly curved posteriorly. Pars facialis of

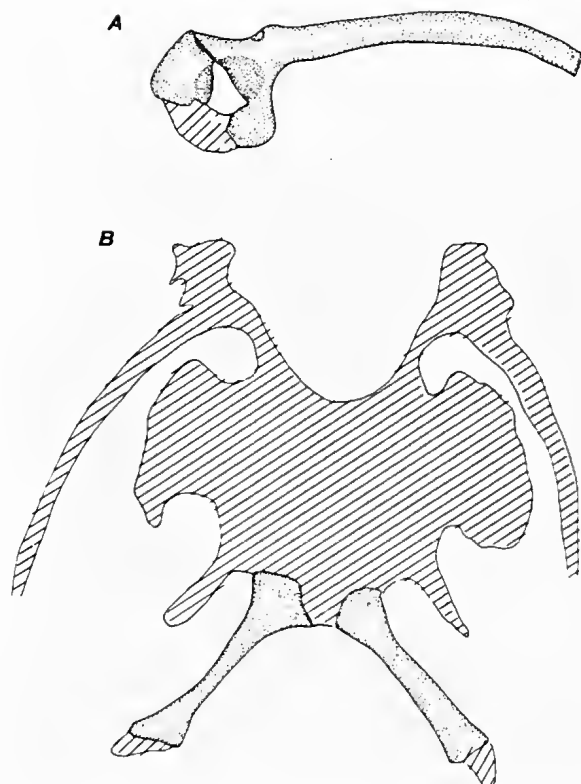


Fig. 31 — *Uperoleia fusca* sp. nov. (SAM R29607). A, Lateral view of ilium. B, ventral view of the hyoid.

maxillary deep then stepped down to become shallow. Preorbital process prominent. Remnant fragments of vomers on edges of choanae and extremities of palatines (Fig. 30). Bony columella present.

Pectoral girdle arciferal and robust. Omosternum absent, xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, closely applied medially. Coracoids robust, widely separated medially. Scapula bicapitate, about same length as clavicles. Suprascapula about $\frac{1}{2}$ ossified.

Eight non-imbricate presacral vertebrae. Sacral diapophyses poorly expanded. Left ilium abnormally enlarged at distal end. Relative widths of transverse processes III > II = sacrum = IV > V = VI = VII = VIII. Crest on urostyle for about $\frac{1}{3}$ its length. Ilium with no dorsal crest. Dorsal prominence very small, slightly rounded with rounded posterolateral dorsal protuberance (Fig. 31). Pubis calcified.

Humerus with strongly-developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3. Distal tips of terminal phalanges knobbed. Carpus of six elements; moderate torsion. O. ulnare and O. radiale present. O. radiale larger of two; both articulate with O. radioulna proximally and with each other medially. Distally both articulate with large transversely-elongate O. centrale postaxiale. O. radiale articulates laterally with O. centrale preaxiale (Fig. 32). O. centrale postaxiale articulates distally with bases of O. metacarpi III, IV and

V. Moderately well-developed flange extends slightly laterally from lateroproximal corner. Palmar sesamoid anteroventrally. O. centrale preaxiale articulates laterally with O. radiale, distally with O. centrale postaxiale and with unfused carpal elements of O. distale carpal 2 and 3 and laterally with basal prepollical element.

Phalangeal formula of foot, 2,2,3,4,3. O. tibiale and O. fibulare elongated elements fused at either end. O. tibiale extends as far as distal end of O. fibulare. Three distal tarsal elements present. Lateral element largest, lying at base of O. metatarsus III, extending laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Second element lies at base of O. metatarsus II. Medial element lies at base of O. metatarsus I, articulating also with O. centrale prehallucis. Distal prepollical element slender and short extending for about $\frac{1}{3}$ length of O. metatarsus I (Fig. 32).

Hyoid plate slightly longer than wide. Anterior hyale expanded anteromedially (Fig. 31). Alary processes not pedunculate. Posterolateral processes moderately slender and elongate. Posterior cornua ossified. Some medial calcification of plate between posterior cornua.

VARIATION: Seventeen of the paratypes have been examined for osteological variation: SAM R29606-7, R29599, R29612-3, R29619, KU 205027, QM J18832, J19927, J27475, J42579, J42598, J42606, J42608, NMV D25045, D25048, D43208.

Medial ossification of the sphenethmoid is incomplete in all of these paratypes. Tenuous contact between the nasals and the sphenethmoid is exhibited by only two paratypes. Separation of the nasals posteromedially varies: in about $\frac{1}{3}$ of the specimens the separation is more extreme and in three specimens it is less than described. The epiotic eminences are extremely prominent in all paratypes except the subadult SAM R29619.

The nature of the pars facialis of the maxillary varies—in some paratypes the shelf is deep initially and then steps down to be shallow anteriorly, in others the decline in depth is gradual and in one specimen (NMV D25048) it remains deep for its entire length.

The alary processes of the premaxillaries are usually moderately broad, but occasionally are broad. Bifurcation of the dorsal extremity varies considerably. The palatines are uniformly truncated laterally. The presence of vomerine fragments varies—they occur in about $\frac{1}{3}$ of the paratypes but the palatal elements are not always apparent bilaterally and in QM J42606 they are relatively large.

In two specimens, the alae of the parasphenoid are curved posterolaterally.

The anterior extremities of the frontoparietals are reduced medially and the frontoparietal fontanelle is barely exposed or unexposed except in the subadult SAM R29619.

ADVERTISEMENT CALLS: Calls of five individuals were recorded at the type locality on 26.i.1984. Call parameters are shown in Table 3 and an advertisement call is shown in Fig. 33. The call is a short rasping note with a duration of about 300 ms pulsed at about 68

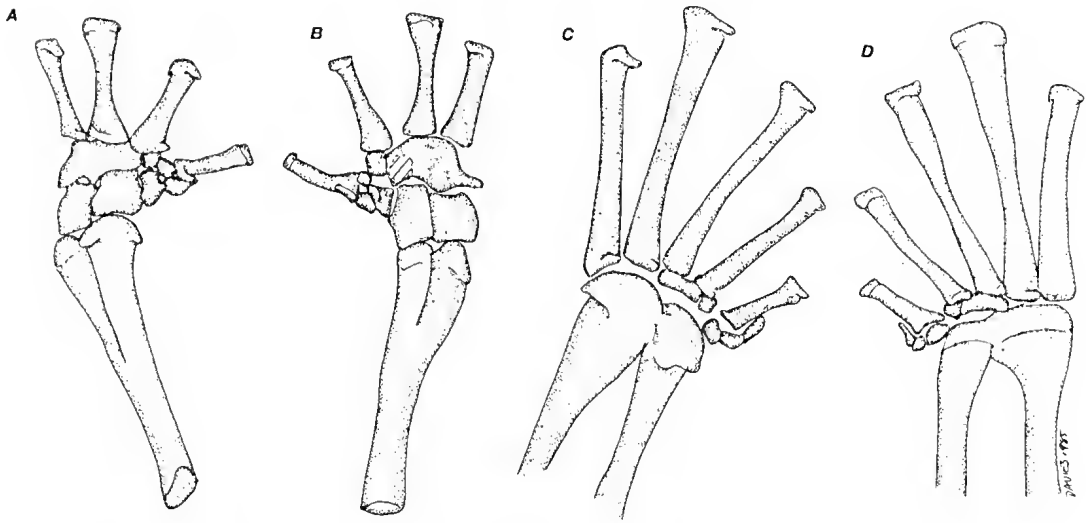


Fig. 32—*Uperoleia fusca* sp. nov. (SAM R29603). A, Dorsal and B, Ventral views of carpus. C, Dorsal and D, Ventral views of tarsus.

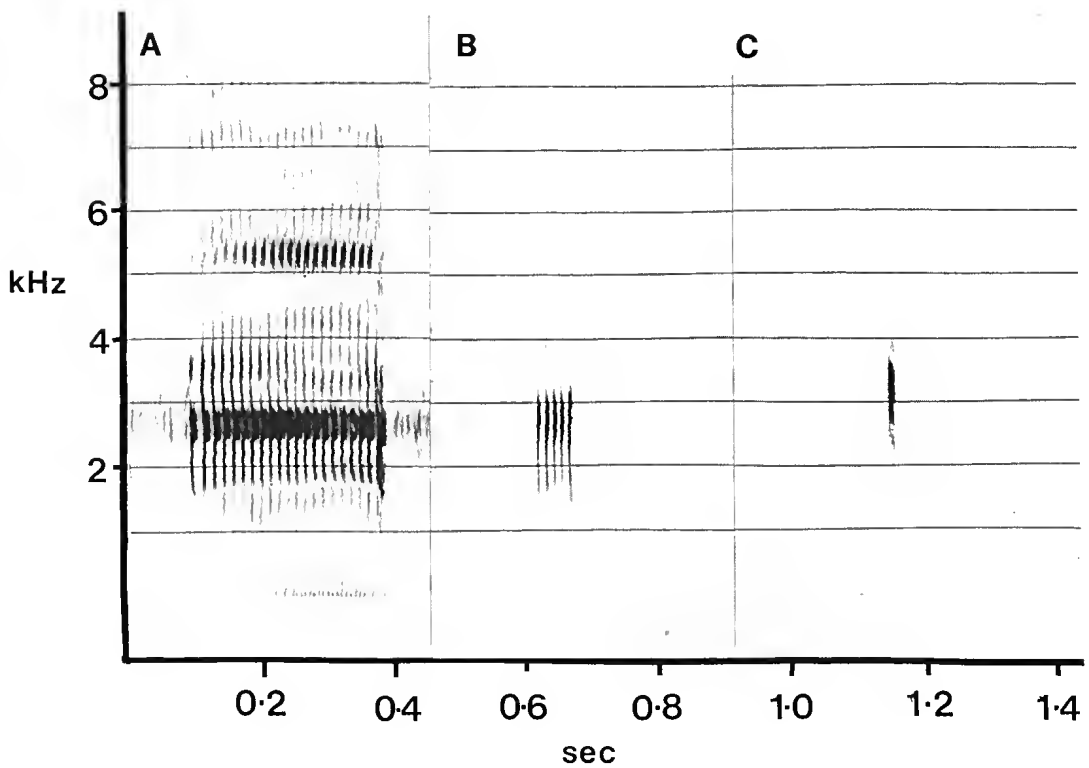


Fig. 33—Sonograms of advertisement calls. A, *Uperoleia fusca* sp. nov. (QM J45961). B, *Uperoleia mimula* sp. nov. (QM J45943). C, *U. lithomoda* (SAM R28771).



Fig. 34—Type locality of *Uperoleia fusca* sp. nov.

pulses sec^{-1} . The dominant frequency lies at about 2700 Hz.

HABITAT: The type locality was a small pond, 30×30 m, surrounded by dry ground covered with sparse low grass to a height of little more than 15 cm (Fig. 34). Frogs were calling at the base of the grass (M. J. Tyler Field notes). The type locality, Mt Glorious, and the Conondale Ranges sites are tall open eucalypt forest with *Themeda australis* understorey. Other localities are open forest with tussock grass understorey except Poona Lake which is surrounded by tall shrubland.

COMPARISON WITH OTHER SPECIES: *Uperoleia fusca* is a moderate sized species (males 20–28 mm S-V, females 23–29 mm S-V), with maxillary teeth and with a poorly-exposed frontoparietal fontanelle. These features are shared by *U. marmorata* and *U. laevisgata*. From *U. marmorata*, *U. fusca* is separated by size (*U. marmorata*, σ 30.1 mm) and by its narrower snout (E-N/IN 1.18 \pm .17 in *U. fusca*, 1.56 in *U. marmorata*).

From *U. laevisgata*, *U. fusca* is separated by total pigmentation of the ventral surface (absent in *U. laevisgata*) and by call. The call of *U. fusca* has 11–28 pulses whereas that of *U. laevisgata* is a longer call of 32–56 pulses (Davies & Littlejohn 1986).

DISTRIBUTION: *Uperoleia fusca* is a coastal species ranging from Gloucester in N.S.W. ($32^{\circ}01'$, $151^{\circ}58'$) to Eungella in Qld ($20^{\circ}55'$, $148^{\circ}30'$) (Fig. 35). Toothed specimens from Atherton held by the Queensland Museum may be referable to this species, but unfor-

tunately are in such poor condition that identification is impossible.

ETYMOLOGY: From the Latin *fuscus* meaning dusky with reference to the ventral pigmentation of the species.

Uperoleia littlejohni sp. nov.

HOLOTYPE: QM J45949 (formerly QNPWS N56317), an adult male collected on Occupational licence 410, Burra Range, Qld ($20^{\circ}33'$, $145^{\circ}05'$) by B. C. Lawrie on 14.xii.1983.

DEFINITION: A moderately-large species (males 22–31 mm S-V, females 23–29 mm S-V) lacking maxillary teeth; possessing unwebbed and poorly-fringed fingers and basal to no webbing and fringed toes. Dermal glands are prominent. Frontoparietal fontanelle moderately extensive; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent. Call not known.

DESCRIPTION OF HOLOTYPE: Maxillary teeth absent. Vomerine teeth absent. Snout short, truncated when viewed from above and in profile. Eye to naris distance greater than internarial span (E-N/IN 1.25) (Fig. 36). Canthus rostralis poorly defined, straight. Tympanum not visible externally (Fig. 36).

Fingers moderately long, broad, unwebbed and poorly fringed with very prominent subarticular tubercles (Fig. 36). In order of length $3 > 4 > 2 > 1$. Palmar tubercles large and prominent. Hind limbs moderately long (TL/S-V 0.34). Toes moderately long,

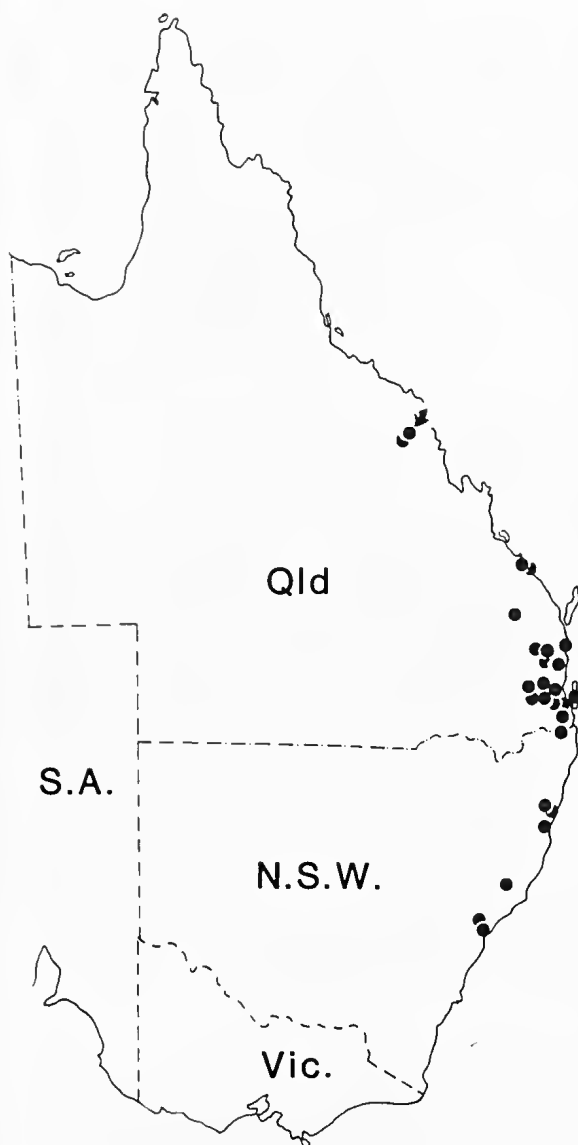


Fig. 35—Distribution of *Uperoleia fusca* sp. nov. The arrow indicates the type locality.

broadly fringed with basal webbing. Toes in order of length $4 > 3 > 5 > 2 > 1$. Metatarsal tubercles very large, raised and prominent; outer elongate, truncate and angled to long axis of foot; inner acutely angled along toe 1 (Fig. 36).

Dorsal surface very faintly tubercular. Parotoid, inguinal and coccygeal glands moderately developed. Submandibular gland disrupted. Cloacal flap slightly fimbriated. Ventral surface faintly granular.

Male with unilobular submandibular vocal sac; unpigmented glandular nuptial pad on thumb. Dorsum grey in preservative with strong chocolate markings, and pinkish-tipped tubercles. Parotoid glands pinkish and inguinal and coccygeal glands with disrupted pinkish patches. Inguinal and post femoral patches white. Ven-

tral surface whitish with suffusions of brown pigment. Throat grey with white granules.

DIMENSIONS (in mm): Snout-vent length 27.6; tibia length 9.5; eye diameter 3.0; eye-naris distance 2.0; internarial span 1.6.

VARIATION: There are 26 paratypes, 24 ♂♂ and 2 ♀♀. All are from Qld. QM J38877-80, 22.4 km W Pentland (20°40', 145°18'), G. Ingram, G. Czechura 15.i.1981; QM J45950, Epping Forest N.P. near Clermont (22°23', 146°42'), G. Porter, D. G. Crossman 12.ix.1984; SAM R29620-1, Gorge Ck (19°33', 143°56'), A. Taplin 18.iii.1984; QM J38883, 18.1 km W Torrens Ck, G. Ingram, G. Czechura 15.i.1981; QM J45953, Battery Station, Snake Creek (145°39', 19°27'), B. C. Lawrie 2.xii.1981; SAM R29622, QM J45952, Caerphilly Station (21°03', 146°05'), B. C. Lawrie 3.iii.1981; KU 205029, CAS 160144, MCZ 108614, QM J45954, SAM R29623, Strathguy (20°57', 144°12'), B. C. Lawrie 24.viii.1984; QM J45951, SAM R29624, Amber Station, about 1.6 km from Frenchs Crossing on Lynd River, K. R. McDonald, S. K. Reardon 15.i.1980; SAM R29625-6, Walsh River, Watsonville (17°21', 145°18'), J. W. Winter 24.xii.1973; QM J43154-5, Walsh River, Jamie Creek, Watsonville, 15.xii.1973; QM J38915, Crest of Warrigal Ra, 16.8 km E Cloncurry, G. Ingram, G. Czechura, 18.i.1981; QM J29874, 96 km from Townsville on Charters Towers Rd, G. Ingram, D. Miller 22.xii.1976; AM R53930, R53932, 6.4 km W Herberton (17°23', 145°23'), J. Barker, G. Grigg 10.i.1974.

All paratypes are moderately robust, slate grey frogs with strong back patterning and conspicuous dermal glands. Paratypes have moderately-long limbs [TL/S-V $0.35 \pm .02$ (0.32-0.41)]. Males range 21.6-30.7 mm S-V and females 23.2-28.8 mm S-V. Eye to naris distance is always greater than internarial span [E-N/IN $1.35 \pm .25$, (1.01-1.64)]. The dorsum is more rugose in a few paratypes and the dermal glands, particularly the coccygeal glands, are more prominent. The parotoid glands are extremely well developed in the larger female (QM J45950). Most of the paratypes, particularly those that are relatively freshly-preserved, show the characteristic salmon pink colouration on the dermal glands and on the tips of dorsal tubercles. The ventral surface is usually a very pale grey with varying suffusions of brown pigment. Colour is apparent in the inguinal and post femoral patches. A pale midvertebral stripe is apparent in some specimens.

OSTEOLOGY (based on SAM R29623): Skull poorly ossified, sloping slightly anteroventrally. Sphenethmoid not ossified medially. Small portion of sphenethmoid ossified posteriorly to anterior extremity of cultriform process of parasphenoid extending about $\frac{1}{3}$ to $\frac{1}{2}$ of length of orbit in ventral view. Prootic not fused with exoccipital. Exoccipital not ossified dorso- or ventromedially. Crista parotica short and stocky, not overlain laterally by otic ramus of squamosal. Very shallow groove of carotid canal posterolaterally on frontoparietals. Frontoparietal fontanelle moderately extensively exposed, vase shaped (Fig. 37). Anterior margin

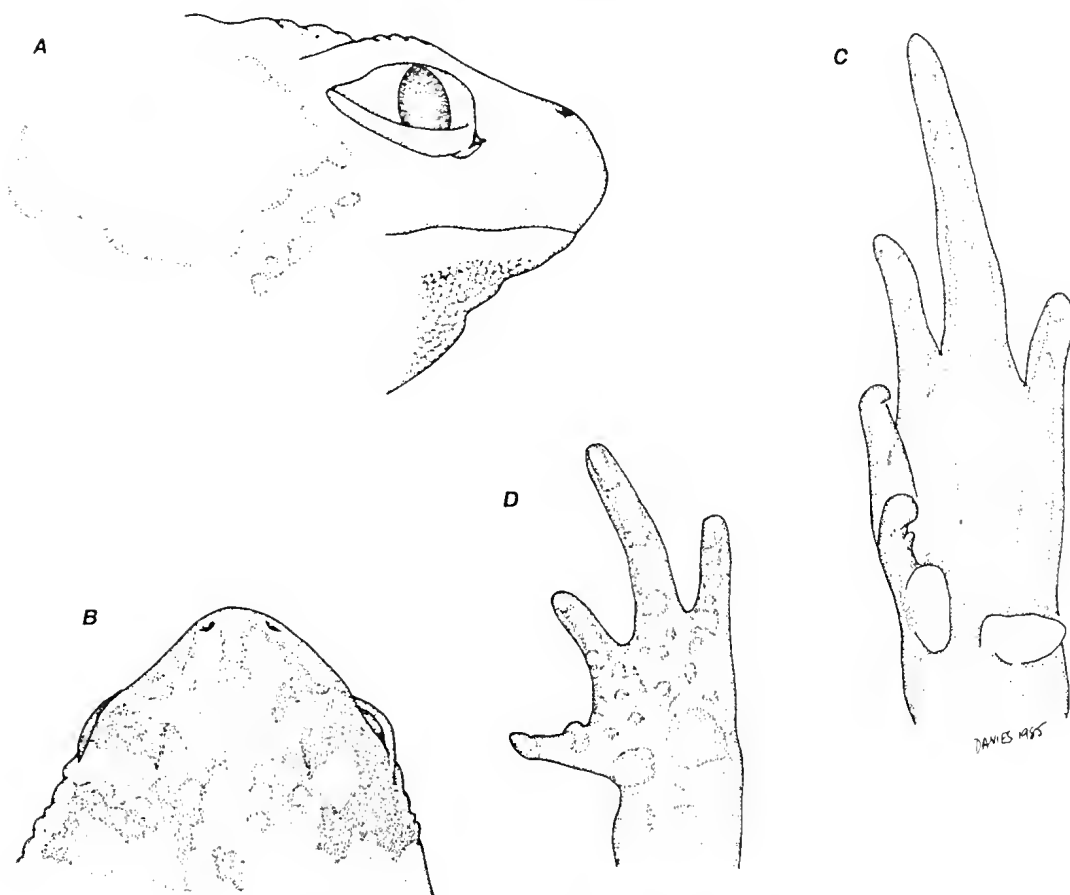


Fig. 36—*Uperoleia littlejohni* sp. nov. A, Lateral and B, Dorsal views of head (QM J38877). C, Plantar view of foot. D, Palmar view of hand (QM J45950).

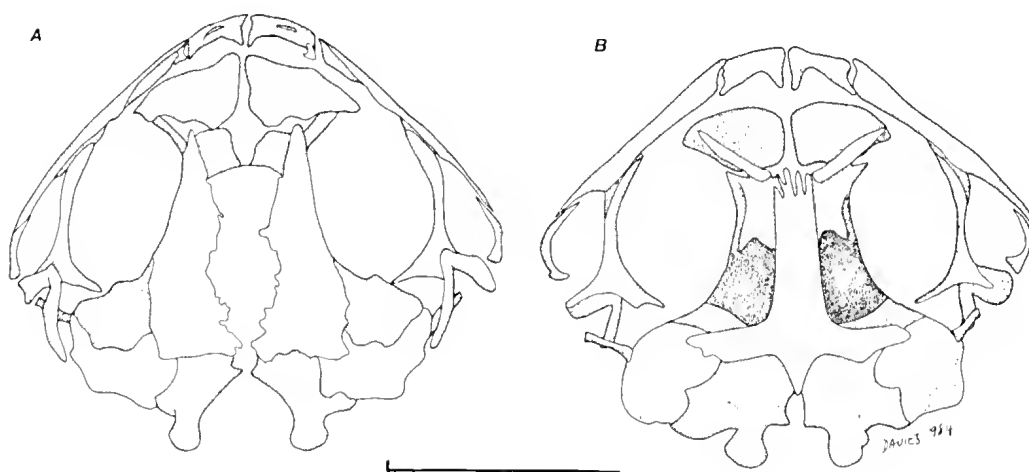


Fig. 37—*Uperoleia littlejohni* sp. nov. (SAM R29623). A, Dorsal and B, Ventral views of skull. Scale bar = 5 mm.

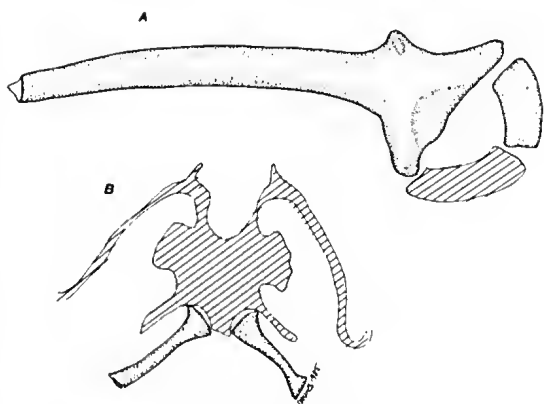


Fig. 38—*Uperoleia littlejohni* sp. nov. (QM J45954). A, Lateral view of ilium. B, Ventral view of hyoid.

defined by sphenethmoid at level about $\frac{1}{4}$ posterior on length of orbit. Posterior margin undefined because of lack of medial ossification of exoccipitals.

Nasals moderately large, approximately triangular. Directed ventrally on lateral extremities; slightly erescenscent on medial anterior edge; in tenuous contact with sphenethmoid posteromedially. Not in contact with frontoparietals. Maxillary processes of nasals truncate, not in contact with moderately-shallow pars facialis of maxillary.

Palatines moderately slender, slightly expanded medially, angled acutely to sphenethmoid (Fig. 37) and totally underlying nasals. Parasphenoid robust. Cultriform process moderately broad, long, anterior extremity divided into digitiform processes (Fig. 37) extending to

level of medial extremities of palatines. Alae moderately narrow, at right angles to cultriform process, not overlapped by medial rami of pterygoids.

Medial rami of pterygoids short, acuminate, not in bony contact with prootic region. Posterior ramus short, moderately broad. Anterior ramus in long contact with well-developed pterygoid process of palatal shelf of maxillary. Cartilaginous quadrate between base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Shaft of squamosal stocky. Zygomatic ramus not developed; otic ramus long, unexpanded.

Maxillary and premaxillary ctenate. Palatal shelf moderately deep with well-developed palatine processes not abutting medially. Pterygoid process well developed. Alary processes of premaxillaries broad at base, narrowing dorsally, bifurcate dorsally, inclined slightly medially. Pars facialis of maxillary moderately shallow; no preorbital process developed. Vomers absent. Bony columella present.

Pectoral girdle arciferal and robust. Omosternum absent, xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, closely applied medially. Coracoids robust, poorly separated medially. Scapula about equal in length to clavicles. Suprascapula about $\frac{1}{2}$ ossified.

Eight nonimbricate presacral vertebrae. Sacral diapophyses poorly expanded. Relative widths of transverse processes III > II > sacrum > IV = V = VI = VII > VIII. Transverse processes on vertebra IV are curved posteriorly. Bicondylar sacrococcygeal articulation. Well-developed crest extending about $\frac{1}{2}$ length of urostyle. Iliac crest absent. Dorsal prominence mon-

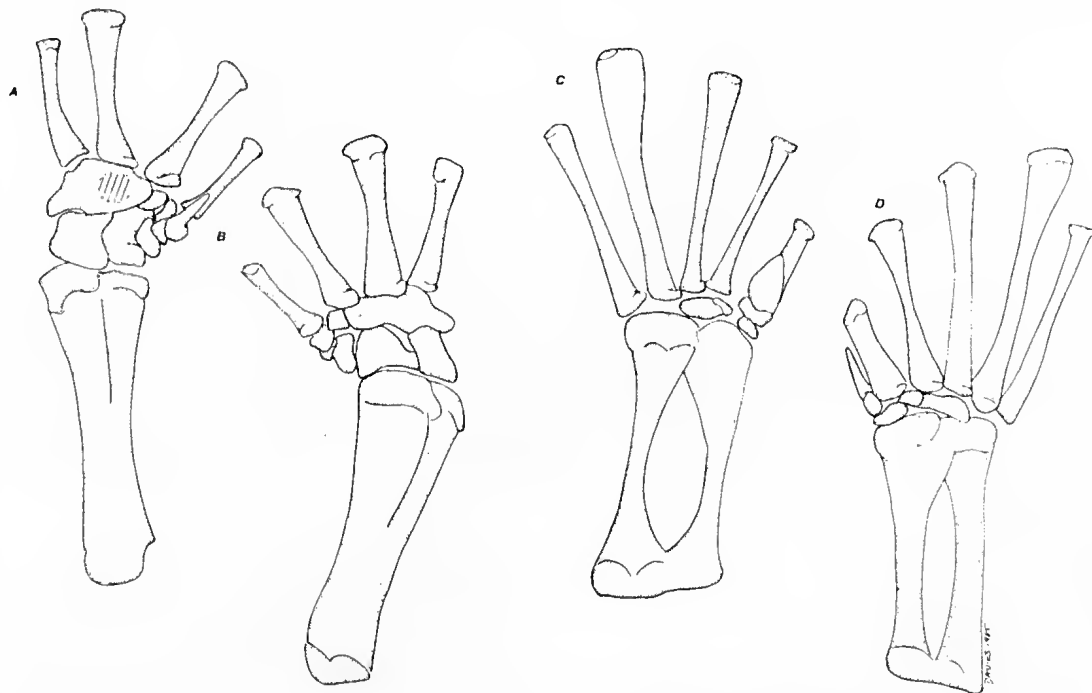


Fig. 39—*Uperoleia littlejohni* sp. nov. (SAM R29622). A, Ventral and B, Dorsal views of carpus. C, Ventral and D, Dorsal views of tarsus.

ticuline; dorsal protuberance mediolateral and prominent (Fig. 38). Pubis clacified.

Humerus with well-developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3. Carpus of six elements. Moderate torsion. O. radiale and O. ulnare present. O. radiale larger of two. Both articulate with O. radioulna proximally and with each other proximomedially. Distally both articulate with large transversely-clongate O. centrale postaxiale. O. radiale articulates laterally with O. centrale preaxiale. O. centrale postaxiale articulates distally with bases of O. metacarpi III, IV and V. Small rounded flange extends proximally onto lateral surface of O. ulnare from lateroproximal corner. Palmar sesamoid ventromedially (Fig. 39). O. centrale preaxiale articulates laterally with O. radiale, distally with O. centrale postaxiale and with carpal elements of O. distale carpal 2 and 3, and laterally with basal prepollical element (Fig. 39). Terminal phalanges knobbed.

Phalangeal formula of foot, 2,2,3,4,3. O. tibiale and O. fibulare elongate, fused at each end. O. tibiale extends to distal end of O. fibulare. Three distal tarsal elements. Lateral element largest, at base of O. metatarsus III; extends laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Second element at base of O. metatarsus II. Medial element at base of O. metatarsus I, articulating with O. centrale prehallucis (Fig. 38). Distal prehallucis element broad and elongate extending greater than $\frac{1}{2}$ length of O. metatarsus I (Fig. 39).

Hyoid plate about as broad as long. Alary processes not pedunculate, moderately broad. Posterolateral processes moderately long and slender. Anteromedial processes of anterior hyale slender. Posterior cornua ossified (Fig. 37).

VARIATION: Nine additional paratypes have been cleared and stained. SAM R29622-4, QM J35427, J45953, J29874, J38880, J38883, AM R53930.

None of the cleared and stained specimens have a preorbital process on the pars facialis of the maxillary. The pars facialis is usually slightly deeper than in the described specimen and occasionally sculptured (QM J29874, SAM R29622). The nasals are not in tenuous contact with the sphenethmoid in QM J38880 and AM R53930, but overlay the sphenethmoid in the two very large specimens SAM R29622, QM J35427. The frontoparietal fontanelle exposure is as described in all but the two large specimens in which the medial constriction is accentuated and the degree of exposure is less overall.

Ventrally the acute angle of the palatines is constant, but the digitiform nature of the extremity of the cultriform process of the parasphenoid is not always present. In one specimen (SAM R29624), the alae of the parasphenoid are angled slightly posterolaterally.

ADVERTISEMENT CALL: The call of this species is not yet known.

COMPARISON WITH OTHER SPECIES: *Uperoleia littlejohni* is an untoothed species with a moderately widely-exposed frontoparietal fontanelle, features shared by *U. crassa*, *U. talpa*, *U. russelli*, *U. glandulosa*, *U. borealis*, *U. arenicola*, *U. inundata* and *U. orientalis*.

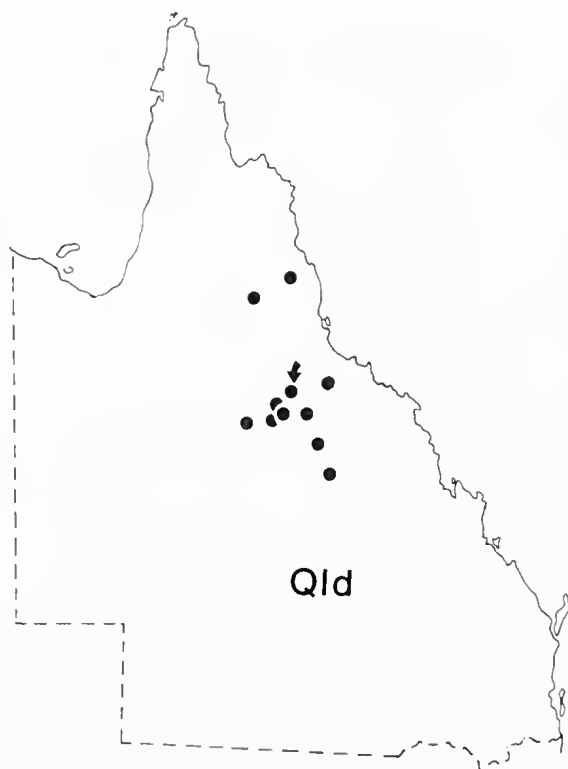


Fig. 40—Distribution of *Uperoleia littlejohni* sp. nov. The arrow indicates the type locality.

From *U. talpa*, *U. russelli*, *U. borealis* and *U. orientalis*, *U. littlejohni* is distinguished by the lack of moderate webbing between the toes. From *U. glandulosa*, *U. littlejohni* is distinguished by the absence of ventral pigmentation, other than faint suffusions and by the absence of lyrate markings on the dorsum and of a well-developed preorbital process of the pars facialis of the maxillary.

From *U. inundata*, *U. arenicola* and *U. crassa*, *U. littlejohni* is distinguished by its strong markings on the dorsum, and by the absence of a preorbital process on the pars facialis of the maxillary.

DISTRIBUTION: *Uperoleia littlejohni* is known only from north eastern and north central Queensland between latitudes 17°–21° (Fig. 40).

ETYMOLOGY: The species is named for Murray J. Littlejohn of the University of Melbourne in recognition of his contributions to the study of herpetology in Australia and of *Uperoleia* in particular.

Uperoleia mimula sp. nov.

Uperoleia marmorata: Parker & Tanner 1971, p. 5.

Uperoleia sp.: Menzies 1977, p. 21; Zweifel & Tyler 1982, p. 764.

U. lithomoda: Tyler & Davies 1984, p. 123 (part.).

HOLOTYPE: QM J45943 (formerly QNPWS N28874), an adult male collected at Lakefield Ranger Station (14°56', 144°12') by K. R. McDonald and B. J. Lyon on 25.ii.1981.

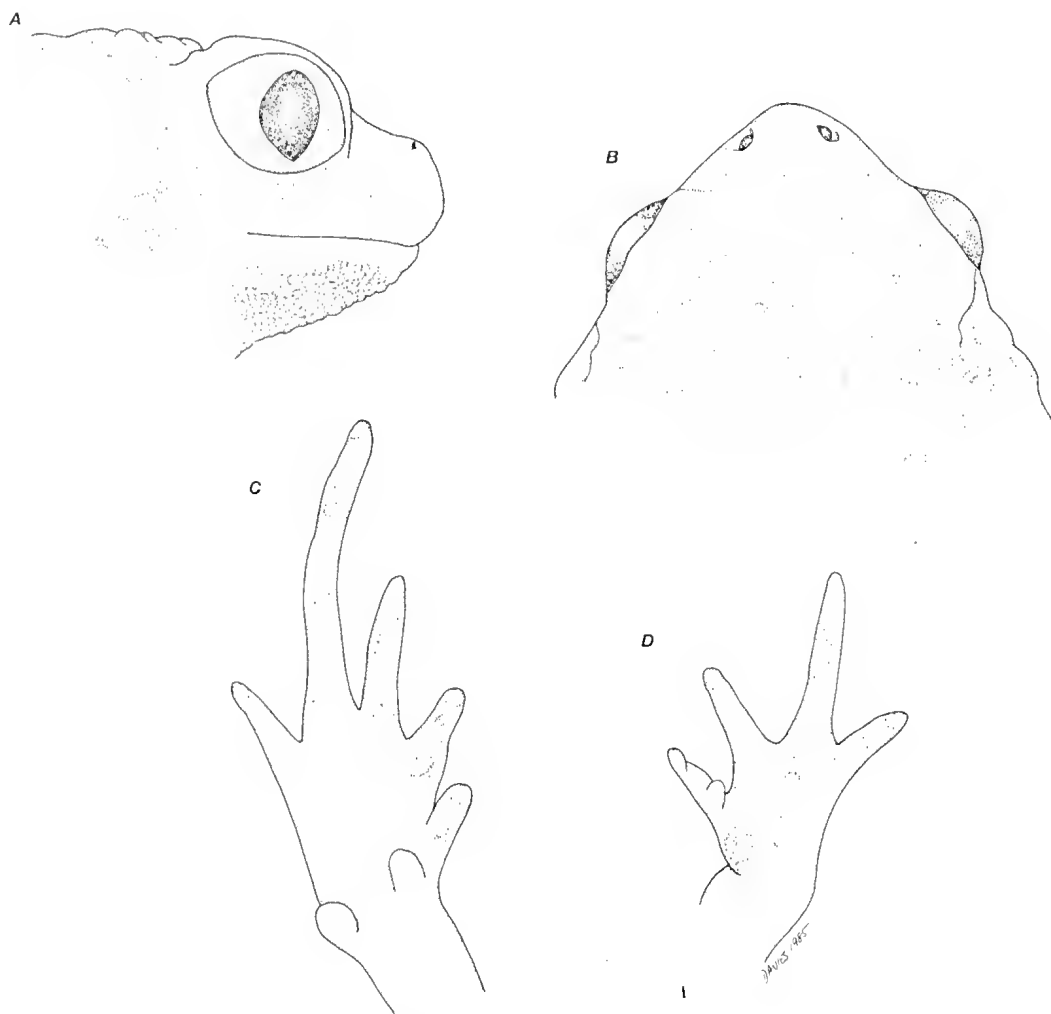


Fig. 41 — *Uperoleia mimula* sp. nov. (holotype). A, Lateral and B, Dorsal views of head. C, Plantar view of foot. D, Palmar view of hand.

DEFINITION: A small to moderate-sized species (males 20–28 mm S-V, females 21–28 mm S-V) with a faintly rugose dorsum; moderately well-developed inguinal glands; toe webbing absent or basal; maxillary teeth absent; poorly- to moderately-exposed frontoparietal fontanelle; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent; male advertisement call a pulsed click of 4–5 pulses, with a pulse repetition rate of about 79 pulses sec^{-1} .

DESCRIPTION OF HOLOTYPE: Maxillary teeth absent. Vomerine teeth absent. Snout short, slightly pointed when viewed from above (Fig. 41), rounded in profile (Fig. 41). Eye to naris distance greater than internarial span (E-N/IN 1.36). Canthus rostralis inconspicuous and straight. Nostrils dorsolateral, surrounded by elevated lip (Fig. 41). Tympanum not visible externally (Fig. 42).

Fingers moderately long, slender, unwebbed, very slightly fringed with prominent subarticular tubercles. In order of length $3 > 4 = 2 > 1$ (Fig. 41). Palmar tubercles moderately large but not prominent. Hind

limbs short (TL/S-V 0.34). Toes long, moderately fringed with trace of basal webbing. Toes in order of length $4 > 3 > 5 > 2 > 1$ (Fig. 41). Metatarsal tubercles prominent. Inner rounded, lying along axis of toe 1; outer rounded, acutely angled to long axis of foot.

Subarticular tubercles moderate, slightly conical. Dorsal surface tubercular. Parotoid glands moderately developed; inguinal glands well developed; coxycal glands prominent. Submandibular gland small, not discrete. Cloacal flap tiny, not fimbriated. Ventral surface faintly granular. Male with unilobular, submandibular vocal sac. Cream glandular nuptial pad on thumb.

Dorsum grey in preservative with faint chocolate patterning and cream tipped tubercles. Prominent midvertebral stripe. Inguinal glands with cream patches along length. Inguinal and femoral patches scarcely detectable, cream. Ventral surface cream with very faint stippling of pigment. Throat stippled with grey.

COLOUR IN LIFE (based on SAM R29634): Inguinal and thigh patches flame scarlet (Smithe 1975). Ground col-

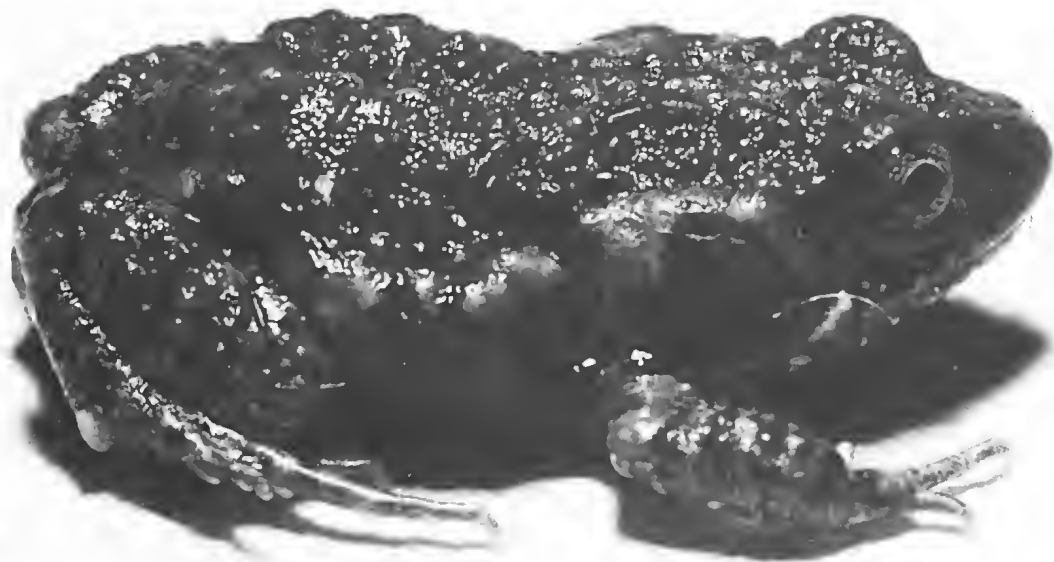


Fig. 42—*Uperoleia mimula* sp. nov. in life, Townsville Common (SAM R29634).

our dull brown with dark chocolate patches upon the head, dorsum and as narrow transverse bars across the limbs. Faint sandy patches upon the parotoids and flanks. Ventrally, densely stippled with dull grey and cream. Throat dark grey in males.

DIMENSIONS (in mm): Snout-vent length 19.9; tibia length 6.7; eye diameter 2.3; eye to naris distance 1.5; internarial span 1.1.

VARIATION: There are 135 paratypes, 125 ♂♂, 7 ♀♀ and 3 subadults.

Qld: SAM R29627 (formerly QNPWS N15605), Lannereost S. F., K. R. McDonald, P. Minton, 16.ii.1984; SAM R29628, Townsville Common, B. J. Lyon, 9.iii.1977; SAM R29629-30, same locality, C. J. Limpus, K. R. McDonald, 10.ii.1977; SAM R29631-40, QM J45946, same locality, K. R. McDonald, 25.xi.1985; QM J45945, Pine River Bay, 22 km NW Rocky Point, Weipa (12°30', 141°43'), J. W. Winter, 13.iii.1983; SAM R29641 (formerly QNPWS N28852), Bazant Outstation, Lakefield N.P., K. R. McDonald, B. J. Lyon 23.ii.1981; KU 205031, SAM R29642, Weipa, K. R. McDonald 3.iii.1981; SAM R29643, Bamaga, B. J. Lyon, C. J. Limpus 14.xii.1976; MCZ 108615, CAS 160145, AMNH 124733, SAM R29644-5, QM J45948, KU 205030, Battery Station nr Snake Creek (19°27', 145°39'), B. C. Lawrie 3.xii.1981; QM J45944, same data, 2.xii.1981; QM J45947, Pajingo Station (20°47', 146°11'), B. C. Lawrie 29.i.1981; SAM R29646, Base of Bluewater Range, K. R. McDonald 3.x.1983; AM R53860-1, Davies Creek Rd, Emerald Creek, 20.8 km SE Mareeba, J. Barker, G. Grigg 2.i.1974; AM R53931, 6.4 km W Herberton, J. Barker, G. Grigg 10.i.1974; AM R62684-5, R62687, Sawmill at Weipa, H. G. Cogger, E. Cameron, P. Webber 8.vii.1977; AM R46278, R46280, R46282-3, R46287, Prince of Wales Is. Torres Strait, P. Webber, E. Cameron, Young 7.ii.1975; AM R46353-92, same data 1.ii.1975; AM R46436-40, same data

11.ii.1975; AM R46460-66, same data 13.ii.1975; AM R46594, same data 15.ii.1975; AM R46931-36, R46937-43, Moa (or Banks) Is. Torres Strait, Webber, Cameron and Young 25.ii.1975; AM R46745-55, same data 21.ii.1975; AM R59167-73, Horn Is, Torres Strait, H. Heatwole, 26.xii.1976; AM R59136, same data, 25.xii.1976; QM J40234, Weipa, G. Ingram 18.iii.1982; QM J40235, J40247, SW North Camp 'Beagle' via Weipa (13°05', 141°57'), G. Ingram 18.iii.1982; QM J42534-5, J42537, 20.8 km, W Cooktown, C. Tanner 1.vi.1974; QM J38271-2, Silver Plains Hstd (13°58', 143°22'), J. Winter *et al.* 15.xii.1978; QM J19859, 4.8 km E Dimbulah, I. R. Straughan; SAM R29647 Lake Louisa (19°54', 144°15'), S. Garnett 18.viii.1984.

All paratypes, with the exception of some material from Battery Station (largest measurements in ranges), are small, not very robust frogs (males 19.9-28.0 mm, females 20.9-28.4 mm) with short hind limbs [TL/S-V 0.34 ± 0.1 (0.31-0.36)]. Eye to naris distance is usually not much greater than internarial span [E-N/IN $1.35 \pm .19$ (1.00-1.82)]. Dermal glands vary in prominence and coloration. Most of the paratypes from Torres Strait tend to have less well-developed and darker dermal glands, although they have consistently lighter-tipped tubercles on the dorsum. Many paratypes have fine suffusions of pigment on the ventral surface. Some paratypes have slightly blunter snouts than the holotype and toe fringing is slightly greater in others. Basal webbing is apparent in very few paratypes. Cream inguinal patches are well developed in many specimens. Material from Townsville Common has granular ventral skin.

OSTEOLOGY (based on SAM R29641): Skull poorly ossified, sloping anteroventrally. Sphenethmoid not ossified medially; small portion ossified posteriorly to distal $\frac{2}{3}$ of palatines and extending about $\frac{1}{3}$ of length of orbit in ventral view. Prootic and exoccipital not fused. Exoccipital not ossified dorsomedially or ventromedially.

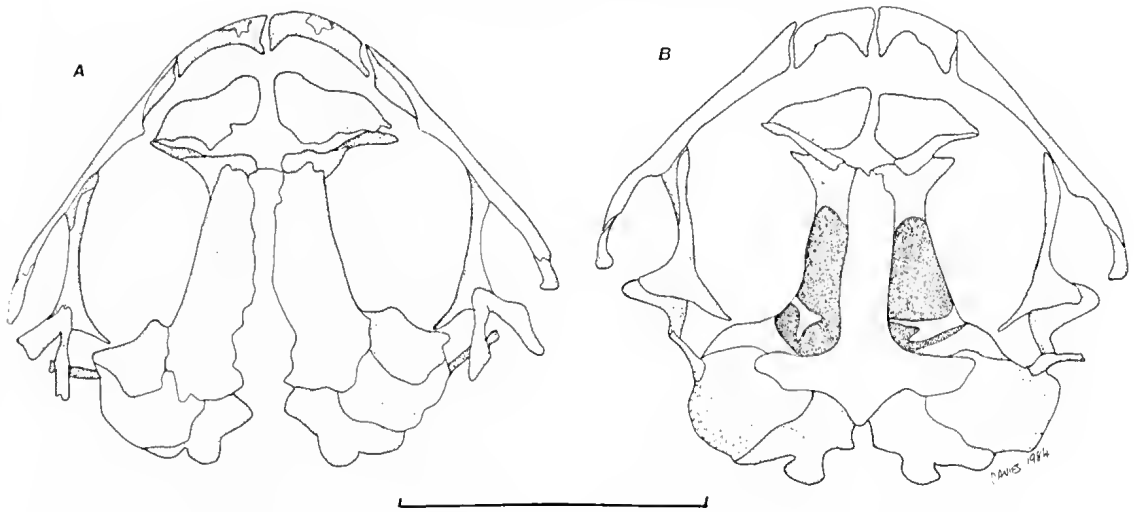


Fig. 43—*Uperoleia mimula* sp. nov. (SAM R29641). A, Dorsal and B, Ventral views of skull. Scale bar = 5 mm.

Crista parotica short, stocky, not articulating with otic ramus of squamosal. Shallow groove for carotid canal present on frontoparietals medial to prominent epiotic eminences. Anterodorsal surface of epiotic eminences expanded into small calcified protuberance. Frontoparietal fontanelle exposed for anterior $\frac{2}{3}$ as moderately-wide slit and for posterior $\frac{1}{3}$ as larger, incomplete, ovoid area. Anterior margin of fontanelle at level of anterior extremities of frontoparietals (Fig. 43). Posterior margin undefined because of lack of medial ossification of exoccipital. Orbital edges of frontoparietal straight, slightly angled posterolaterally.

Nasals moderately-well ossified, curved ventrally on lateral extremities and with crescentic medial anterior edge; widely separated posteromedially (Fig. 43). Nasals not in bony contact with sphenethmoid or frontoparietals. Maxillary process of nasal moderately acuminate, widely separated from well-developed pre-orbital process of shallow pars facialis of maxillary.

Palatines slender, slightly expanded medially, tapered laterally; reduced laterally, not extending beyond maxillary processes of nasals. Parasphenoid robust with long, moderately-slender cultriform process reaching between medial extremities of palatines. Alae moderately short, moderately slender, not overlain by medial ramus of pterygoid.

Medial ramus of pterygoid moderately long, acuminate, not in bony contact with prootic region; posterior ramus short, broad; anterior ramus expanded anteriorly, in long contact with moderately well-developed pterygoid process of palatal shelf of maxillary. Cartilaginous quadrate present at base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Squamosal shaft robust, zygomatic ramus minute; otic ramus short, unexpanded.

Maxillary and premaxillary edentate. Palatal shelf moderately deep with well-developed palatine processes not abutting medially. Pterygoid process moderately

well developed. Alary processes of premaxillaries slender, bifurcate, inclined posteromedially. Vomers absent. Bony columella present (Fig. 43).

Pectoral girdle arciferal and robust. Omosternum and xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, poorly separated medially. Coracoids robust, moderately separated medially. Scapula bicapitate, about same length as clavicles. Suprascapula about $\frac{1}{3}$ – $\frac{1}{2}$ ossified.

Eight non-imbricate presacral vertebrae. Sacral diapophyses poorly expanded. Relative widths of transverse processes $\text{III} > \text{IV} > \text{sacrum} > \text{II} = \text{V} = \text{VI} > \text{VII} > \text{VIII}$. Urostyle bicondylar with dorsal crest extending approximately half its length. Iliac crest absent. Dorsal prominence wedge shaped, very prominent. Dorsal protuberance conical, anterolateral and prominent (Fig. 44).

Humerus with strongly-developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3. Carpus of six

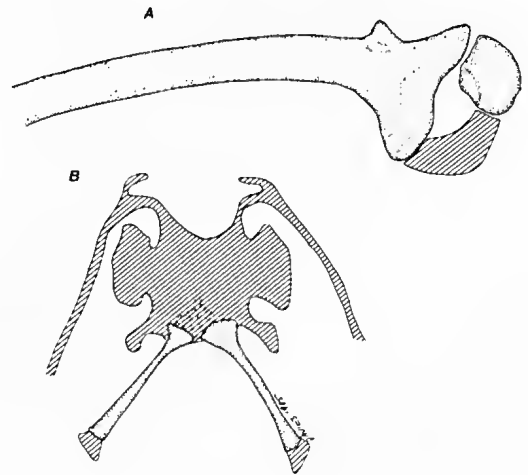


Fig. 44—*Uperoleia mimula* sp. nov. (AM R46750). A, Lateral view of pelvis. B, ventral view of hyoid.

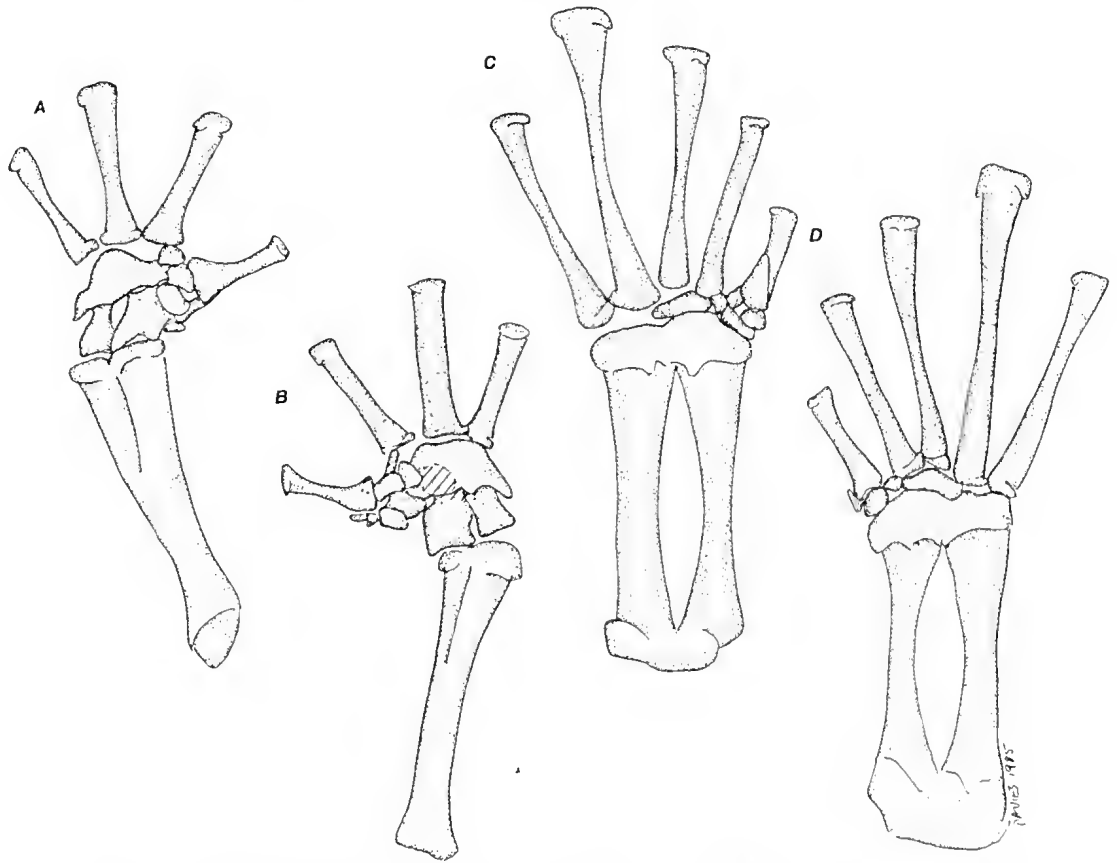


Fig. 45—*Uperoleia mimula* (SAM R29641). A, Dorsal and B, Ventral views of carpus. C, Ventral and D, Dorsal views of tarsus.

elements; considerable torsion. O. radiale and O. ulnare present. O. radiale larger of two. Both elements articulate with O. radioulna proximally and with each other proximomedially. Distally both articulate with large, transversely-elongated O. centrale preaxiale. O. centrale postaxiale articulates distally with bases of O. metacarpi III, IV and V. Moderately well-developed flange extends proximally from lateroproximal corner. Palmar sesamoid proximomedially on ventral surface. O. centrale preaxiale articulates laterally with O. radiale, distally with O. centrale postaxiale and with carpal element of O. distale carpal 2, laterally with basal prepollical element. Carpal element of O. distale carpal 2 articulates with carpal element of O. distale carpal 3. Distal tips of terminal phalanges knobbed.

Phalangeal formula of foot 2,2,3,4,3. O. tibiale and O. fibulare elongate and fused at either end. O. tibiale extends as far as distal end of O. fibulare. Three distal tarsal elements present. Lateral element largest, lying at base of O. metatarsus III and extending laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Second element lying at base and slightly lateral to O. metatarsus II. Medial element lying at base of O. metatarsus I and articulating with O. centrale prehallucis (Fig. 45). Distal prehallucal element large and pear shaped, extend-

ing approximately half length of O. metatarsus I (Fig. 45).

Hyoid plate approximately as long as broad. Antero-medial processes of anterior hyale slender and oriented medially. Posterolateral process of hyoid plate moderately broad and moderately short. Alary processes not pedunculate. Posterior cornua ossified. Posteromedial portion of plate slightly calcified (Fig. 44).

VARIATION: A further 23 paratypes have been cleared and stained: SAM R29642-3, R15410, R29631-3, R29645-6, QM J38271, J45947, J45948, AM R62685, R46280, R46282, R46283, R46364, R46380-1, R46437, R46746, R46932, R46934, R46390.

Three osteological features are consistent within the material examined, namely, the length and shape of the palatine processes of the premaxillaries; the length of the otic ramus of the squamosal (the shape varies occasionally with some specimens showing some expansion of the ramus); and, the tiny process on the anterodorsal surface of the epiotic eminences.

The crescentic indentation on the anterior edge of the nasals as exhibited in SAM R29641 is unique to that specimen and those from Townsville Common—all other specimens lack this feature. The shape of the pterygoid and, in particular, the slender, acuminate and acutely-angled medial process is exhibited only by SAM

R29641. The shape of the medial ramus of the pterygoid is highly variable amongst the material examined but in all cases is more robust than shown in Fig. 43.

The truncated nature of the anterior extremities of the frontoparietals is unusual, other specimens having anterolateral extensions to these bones. Exposure of the frontoparietal fontanelle varies, with very few specimens lacking the posterior expansion, but most having more crenate medial edges to the frontoparietals.

The nature of the frontoparietal fontanelle exposure is unusually variable in this species. It is poorly exposed in material from Townsville Common.

HABITAT: Found in *Melaleuca* woodland, eucalypt open woodland and woodland with tussock grassland. Frogs often shelter beneath leaf and stick litter when calling. They call from the edge of the water or up to 12 metres away.

ADVERTISEMENT CALL: The call of *U. mimula* is a short 3-5 pulsed signal with a pulse repetition rate of 75.9 sec^{-1} and a dominant frequency of 2816 Hz (see Table 3, Fig. 32).

The call is longer than, but to the ear resembles that of, the sympatric *U. lithomoda*, particularly at high temperatures (Table 3, Fig. 32). The description of the call of *Uperoleia* on Horn Island by F. Parker as a 'click' (Tyler & Davies 1984) and the close morphological similarity between *U. mimula* and *U. lithomoda* has led to the misidentification of this material.

COMPARISON WITH OTHER SPECIES: *Uperoleia mimula* is an untoothed species with a poorly- to moderately-exposed frontoparietal fontanelle, features shared only by *U. lithomoda* and *U. capitulata*.

From *U. lithomoda*, *U. mimula* is distinguished by a lack of strong dorsal patterning, by the presence of pigmentation on the ventral surface, by poor to moderate development of the inguinal glands and by call (the call of *U. mimula* is clearly pulsed to the ear, whereas that of *U. lithomoda* is a sharp click—see Table 3, Fig. 33).

From *U. capitulata*, *U. mimula* is distinguished by the absence of fringing on the fingers, a tubercular dorsum and less ossification of the nasals, and the presence of a preorbital process on the pars facialis of the maxillary.

DISTRIBUTION: *Uperoleia mimula* is confined to the Cape York Peninsula and Torres Strait Islands, extending as far south as Townsville (Fig. 46). It also occurs in New Guinea at Morehead.

ETYMOLOGY: From the Latin *mimula* meaning an actor or mimic with reference to the similarity in morphology and call of this species to its sympatric congener *U. lithomoda*.

COMMENT: Tyler and Davies (1984) assigned specimens of *U. mimula* to *U. lithomoda* on the basis of external morphology, osteology and verbal call description. Our studies have shown these two species to be difficult to separate other than on the basis of call. The specimen illustrated by Parker and Tanner (1971) from Horn Island (MCZ 80234) appears to resemble *U. lithomoda* in life (see Fig. 2). However, the preserved specimen resembles *U. mimula* in external morphology. Variation in

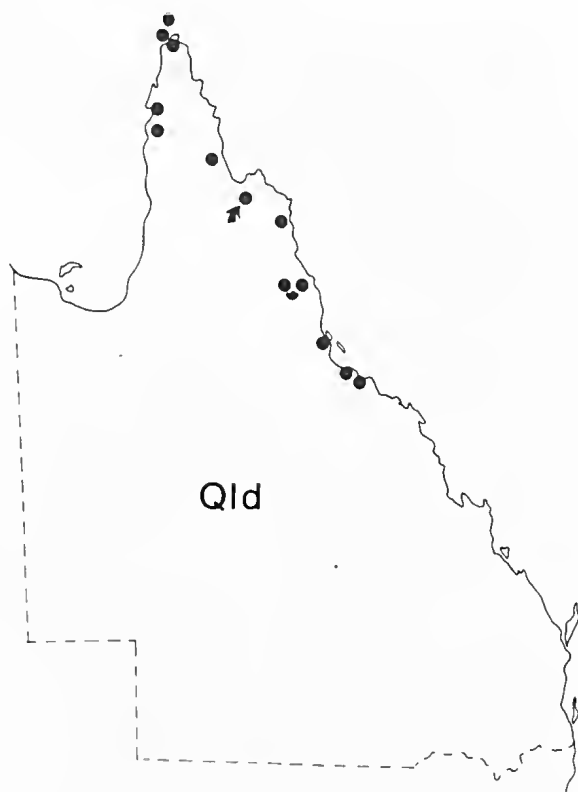


Fig. 46—Distribution of *Uperoleia mimula*. The arrow indicates the type locality.

osteology of *U. lithomoda* (see p. 148) now known to occur is a major contributing factor to misidentification of this material.

The specimens from New Guinea examined by Tyler and Davies (1984) are osteologically closer to *U. mimula* than *U. lithomoda*. These specimens do, however, have extremely prominent inguinal and femoral patches characteristic of neither species. They are assigned here to *U. mimula* on the basis of their osteology, but excluded from the type series.

DISCUSSION

With the description of eastern Australian taxa of *Uperoleia* now largely completed, it becomes possible to examine the value of external morphology and of osteology in delimiting species in this exceptionally conservative, yet extremely speciose, genus. *Uperoleia* now comprises 23 species and it is likely that further species remain undefined.

The value of call in identifying species in *Uperoleia* has been shown by Davies and Littlejohn (1986). It is clear that *Uperoleia* contains a number of sibling species and that call data will remain essential in the elucidation of these and other taxa as yet undescribed. *Uperoleia inundata* and *U. arenicola* are separable only by call, and call is important in separating some *U. laevigata* and *U.*

fusca, *U. lithomoda* and *U. mimula*, and *U. tyleri* and *U. martini*.

External morphology must be used in conjunction with call data and becomes important when call data are not available. As has been shown here and elsewhere (Tyler *et al.* 1981a,b,c, Davies & Littlejohn 1986) morphology is extremely conservative in *Uperoleia* and many features show intraspecific variation necessitating an understanding of morphological variation across the range of the species.

Size has been considered a useful character in delimiting *Uperoleia* (Tyler *et al.* 1981a) and it remains so for very small and very large species. However, our data for *U. lithomoda* show size differences between different populations that, taken in isolation, could be misleading. Specimens of *U. lithomoda* on Groote Eylandt are large, larger than those from any other locality except the Lennard River region of W.A., whereas specimens of *U. lithomoda* from Edward River on the west of Cape York, are small, smaller than *U. lithomoda* from any other locality except the Mary River environs on the Arnhem Highway. The Mary River material is smaller than Amber Station and Lennard River frogs. Clearly there is no geographic cline in these data. Davies and Littlejohn (1986) noted size differences in *U. rugosa* that were associated with locality.

Size differences between species are useful in defining small species such as *U. mjobergi* (Tyler *et al.* 1981c and unpubl. data) and large species such as *U. tyleri* (Davies & Littlejohn 1986) but should be treated with caution in species with a wide geographic range.

Snout shape is considered to be a consistent species-specific character in certain Middle American hylids (Duellman, 1970) but our studies have shown variability in this feature in *Uperoleia* even at one site. Snout shape is extremely sensitive to preservation techniques and strong preservative can distort a rounded snout to the truncated condition. Thus the state of preservation of the specimen should be taken into account when examining snout shape.

Some features, such as the condition of dermal glands, show temporal variation, but the location and general extent of glands appear to be good species indicators. The function of the dermal glands is not known. The secretion from these glands may be distasteful or toxic to predators. However, examination of the stomach contents of Rufous (Nankeen) night herons (*Nycticorax caledonicus*) taken feeding on frogs at Derby airport, showed considerable numbers of *U. mjobergi* in the stomach (Tyler & Davies unpubl.). However, the other two local species, *U. talpa* and *U. aspera*, were not represented in the prey. *U. talpa* is unique amongst *Uperoleia* in that it releases copious quantities of a white frothy secretion from the parotoid glands under conditions of minimal stress. This substance is toxic to other frogs sharing the same container (Tyler, Davies, Martin & Watson unpubl.). We do not know of this phenomenon in any other species of *Uperoleia*. As indicated earlier, *Denisonia devisi* has been observed feeding on *U. capitulata*.

The activity, and thus the external appearance, of dermal glands appears to be seasonal as shown by the poor development of these features in specimens of *U. lithomoda* dug from the vegetable garden of Gibb River Station homestead during the dry season. Hypertrophy of parotoid and inguinal glands occurs in isolated specimens of most species studied, and is a feature of *U. capitulata*. Likewise hypertrophy of the parotoid glands is a feature of *U. tyleri* and *U. martini* (Davies & Littlejohn 1986).

Rugosity of the dorsum is a reliable character at the extremes of expression i.e. smooth or tubercular. Intermediate conditions are difficult to quantify. The fine conical tubercles on the dorsum of *U. trachyderma* are an excellent indicator for this species and are unique within the genus. Granularity of the ventral surface can vary, but is usually consistent. Variation may be sexual, but our data are inconclusive.

Dorsal colour patterning is a useful character provided that the limits of variability are established. Scapular plicae, golden glands, strong dark patterns or poor pattern are all species specific.

Subarticular and palmar tubercles can vary slightly. Palmar tubercles, particularly at the base of the thumb, are rarely prominent and in males are usually masked by the unpigmented glandular nuptial pad of the thumb. Supernumerary tubercles on the palm are common and vary in degree of development. Fringing on the fingers is rare and is a consistent feature in those species exhibiting it.

Toe fringing varies slightly within a species, but is generally a good character. Toe webbing is variable, but is a good feature if the extent of variability is defined. The condition of the subarticular tubercles of the toes appears constant, but is very conservative. However, the size, state and orientation of the inner and outer metatarsal tubercles can vary and in some cases these are good species indicators.

Ventral pigmentation is a reliable character. It is the only consistent feature useful in separating *U. laevigata* and *U. fusca*. It can be extremely variable in form (e.g. *U. laevigata*) or extremely constant (e.g. *U. fusca*, *U. tyleri*, *U. martini*) but recognition of the limits of variability of the feature allows its usefulness to be exploited. Colour in life of inguinal and post femoral patches is a good species indicator except in *U. fusca* where two distinct colour forms are known to occur. Unfortunately, this feature is fugitive, and is rarely recorded by collectors.

It is clear, then, that species can be grouped on a combination of morphological features, but such groupings rely heavily on knowledge of the extent of variability within any one species.

Davies and Littlejohn (1986) considered the value of osteological features in delimiting species of *Uperoleia*. In the main, our data support their conclusions. The most useful osteological feature in recognition of species in *Uperoleia* is the condition of the exposure of the frontoparietal fontanelle. However, our data on *U. lithomoda* show that this feature is subject to variation

and that ontogenetic effects must be taken into consideration. The osteological definition of a species must take account of a number of features in common, including the frontoparietal fontanelle exposure. For instance, in *U. lithomoda*, the crescentic shape of the anterior edge of the nasals and the anteromedial curvature of the orbital edges of the frontoparietals together with the poor to moderate exposure of the frontoparietal fontanelle are a combination of features unique to this species.

The condition of the distale carpalia 2 and 3 is a useful postcranial osteological feature. Three conditions occur in *Uperoleia*: the elements are fused, as in *U. rugosa*, *U. trachyderma* and *U. capitulata*; closely applied as in *U. tyleri*, *U. martini*, *U. fusca*, *U. nimula*, *U. littlejohni* and *U. inundata*; or, free as in *U. lithomoda* and *U. laevigata*. In those species in which the elements are closely applied, fusion occurs in isolated specimens (e.g. *U. tyleri*, Davies unpubl.).

The hyoid shows variability in the presence or absence of anteromedial processes on the anterior hyale. These processes are slender and short in all *Uperoleia* reported so far except *U. laevigata*, *U. fusca*, *U. tyleri* and *U. martini*. In these species, the processes appear to be absent and the anteromedial portion of the anterior hyale is thickened. All of these species share a dentate maxillary arch. However, the dentate northwestern species, *U. mjobergi*, has slender anteromedial processes on the anterior hyale (Davies unpubl.) and hence association of the lack of processes with dentate species occurs only in the eastern portion of the continent.

The features of the ilium appear to be species-specific and to be indicators of species relationships. The dorsal prominence has been reported as papillate in *U. glandulosa* (Davies *et al.* 1985), is tiny and rounded in *U. rugosa*, *U. laevigata* and *U. fusca*, is very prominent and wedged-shaped in *U. nimula* and *U. lithomoda* and mon-

ticuline in *U. tyleri*, *U. martini*, *U. trachyderma*, *U. capitulata* and *U. littlejohni*. The dorsal protuberance is anterolateral, lateral or posterolateral. The presence of a small ilial crest in *U. trachyderma* is unusual, a feature shared only by *U. micromeles* (Davies unpubl.).

The distribution of many species of *Uperoleia* in Queensland conforms largely to the major biogeographic boundaries proposed by Stanton and Morgan (1977). *Uperoleia littlejohni* is confined to the Desert and Einasleigh Uplands, a region that is distinctly drier, more generally elevated and more lightly timbered than Cape York Peninsula (Stanton & Morgan 1977). *U. inundata* intrudes into Queensland at Westmoreland where presumably the predominantly sparse woodland and lagoons approximate the habitat occupied by this species in coastal Northern Territory.

U. rugosa is found in the Brigalow Belt, Mulga Lands and south east Queensland region, as well as west of the Great Dividing Range in N.S.W., showing a diversity of habitat throughout its wide distribution, whereas *U. capitulata* is confined to the Mulga Lands and Channel Country complex where it is sympatric with *U. rugosa* at some sites.

U. fusca is a Central Coast Rainforest and South East Queensland species extending coastally to northern N.S.W. whereas its cryptic congener *U. laevigata* is found along the Great Dividing Range.

U. nimula, although found mainly on Cape York, has a broader habitat distribution extending to the Einasleigh Uplands and the wet tropical rainforests.

The regions of Stanton and Morgan (1977) are broadly based, and the distribution of species of *Uperoleia* within these regions is probably highly selective. *U. trachyderma* is known only from grey self-mulching cracking clays, but the association of other congeners with a particular soil type has not been documented. However, *U. lithomoda* is associated with

KEYS

Regional keys are useful in identifying material within this genus. Thus we present firstly a key to *Uperoleia* in the eastern states and then a key to the genus.

KEY TO *Uperoleia* IN EASTERN AUSTRALIA:

1. Maxillary arch dentate 2
Maxillary arch edentate 5
2. Ventral surface fully pigmented 3
Ventral surface never fully pigmented *U. laevigata*
3. Parotoid glands hypertrophied 4
Parotoid glands not hypertrophied *U. fusca*
4. Dorsum smooth, not flecked with light pigment *U. tyleri*
Dorsum rugose, flecked with light pigment *U. martini*
5. Dorsum covered with fine conical tubercles *U. trachyderma*
Dorsum not covered with fine conical tubercles 6
6. Parotoid, inguinal and coeeygeal glands prominent 7
Parotoid, inguinal and coeeygeal glands not prominent 10
7. Parotoid glands hypertrophied, head small, skin relatively smooth *U. capitulata*
Parotoid glands not hypertrophied, skin rugose 8
8. Dermal glands prominently yellow tipped, providing prominent lateral stripes *U. lithomoda*
Dermal glands not prominently yellow tipped, no prominent lateral stripes 9
9. Dorsum rugose, back pattern strong, ventral surface faintly granular *U. rugosa*
Dorsum poorly rugose, back pattern weak, ventral surface smooth *U. nimula*
10. Dorsal pattern discrete, tubercles pink tipped, parotoid glands rarely prominent *U. littlejohni*
Dorsal pattern never discrete, not prominent, parotoid glands prominent *U. inundata*

KEY TO THE GENUS *Uperoleia* IN AUSTRALIA:

1. Internarial span less than eye to naris distance	2
Internarial span greater than eye to naris distance	<i>U. micromeles</i>
2. Maxillary arch dentate	3
Maxillary arch edentate	8
3. Prominent papilla on heel present	<i>U. mjobergi</i>
Prominent papilla on heel absent	4
4. Ventral surface fully pigmented	5
Ventral surface not fully pigmented	7
5. Parotoid glands hypertrophied	6
Parotoid glands not hypertrophied	<i>U. fusca</i>
6. Dorsal surface dark, parotoid glands not pigmented	<i>U. tyleri</i>
Dorsal surface flecked with light pigment, parotoid glands flecked with light pigment ...	<i>U. martini</i>
7. Yellowish triangular patch on head	<i>U. laevigata</i>
Greenish triangular patch on head	<i>U. marmorata</i>
8. Toes moderately webbed	9
Toes unwebbed or basally webbed	12
9. Dorsal surface tubercular	10
Dorsal surface smooth or only faintly tubercular	11
10. Parotoid glands prominent, scapular plicae present	<i>U. russelli</i>
Parotoid glands moderately prominent, scapular plicae absent	<i>U. borealis</i>
11. Mid-vertebral stripe absent; faint dorsal pattern	<i>U. talpa</i>
Mid-vertebral stripe present; no dorsal pattern	<i>U. orientalis</i>
12. Both inner and outer metatarsal tubercles raised and prominent	13
Outer metatarsal tubercle small and poorly raised	<i>U. trachyderma</i>
13. Frontoparietal fontanelle widely exposed	14
Frontoparietal fontanelle not widely exposed	18
14. Ventral surface unpigmented	15
Ventral surface pigmented	16
15. Nasals moderately ossified	<i>U. inundata</i>
Nasals poorly ossified	<i>U. arenicola</i>
16. Dorsum with strongly-developed pattern	17
Dorsum with indistinct pattern	<i>U. crassa</i>
17. Toes well fringed and moderately basally webbed	<i>U. glandulosa</i>
Toes poorly fringed and poorly basally unwebbed	<i>U. littlejohni</i>
18. Mating call a sharp click, ventral surface unpigmented	19
Mating call a pulsed note, ventral surface pigmented	21
19. Well-developed parotoid glands and well or moderately developed inguinal and coccygeal glands	20
Moderately developed parotoid glands, poorly developed inguinal and coccygeal glands	<i>U. minima</i>
20. Dorsal pattern strongly defined, inguinal glands hypertrophied	<i>U. lithomoda</i>
Dorsal pattern not strongly defined, inguinal glands not hypertrophied	<i>U. aspera</i>
21. Frontoparietal fontanelle moderately exposed; dorsal surface faintly rugose	22
Frontoparietal fontanelle unexposed; dorsal surface moderately rugose	<i>U. rugosa</i>
22. Parotoid, inguinal and coccygeal glands hypertrophied	<i>U. capitulata</i>
Parotoid, inguinal and coccygeal glands not hypertrophied	<i>U. mimula</i>

still ephemeral waters, and *U. borealis* with streamside habitats (Tyler, Watson & Davies unpubl. data). It is likely, then, that microhabitat is extremely important in these small fossorial species.

It is probable that further species of *Uperoleia* occur in eastern Australia, but lack of collecting in particular areas and lack of call data from many specimens preclude description of these taxa at this time. The collection of *Uperoleia* is a fortuitous event—calling males are difficult to locate because of their innate ventriloquial abilities and the absence of calling activity except after rain. The size and drab appearance of foraging individuals and the long periods of time spent underground all contribute to the sparse data available on this genus, particularly from remote areas. Since many habitats are difficult, if not impossible, to visit at

times of maximal frog activity, the elucidation of the boundaries of this large and morphologically conservative genus remains unknown.

CHECKLIST OF *Uperoleia* GRAY (Sequence chronological): *Uperoleia marmorata* Gray 1841

Uperoleia laevigata Keferstein 1867

Uperoleia mjobergi (Andersson, 1913)

Uperoleia rugosa (Andersson, 1916)

Uperoleia russelli (Loveridge, 1933)

Uperoleia orientalis (Parker, 1940)

Uperoleia arenicola Tyler, Davies and Martin, 1981a

Uperoleia borealis Tyler, Davies and Martin, 1981a

Uperoleia crassa Tyler, Davies and Martin, 1981a

Uperoleia inundata Tyler, Davies and Martin, 1981a

Uperoleia lithomoda Tyler, Davies and Martin, 1981a

Uperoleia micromeles Tyler, Davies and Martin, 1981a

Uperoleia minima Tyler, Davies and Martin, 1981a
Uperoleia talpa Tyler, Davies and Martin, 1981a
Uperoleia aspera Tyler, Davies and Martin, 1981b
Uperoleia trachyderma Tyler, Davies and Martin, 1981c
Uperoleia glandulosa Davies, Mahony and Roberts, 1985
Uperoleia martini Davies and Littlejohn 1986
Uperoleia tyleri Davies and Littlejohn 1986
Uperoleia capitulata sp. nov.
Uperoleia fusca sp. nov.
Uperoleia littlejohni sp. nov.
Uperoleia mimula sp. nov.

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